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September 1985

Marine Flora and Fauna of the Northeastern United States. Echinodermata: Echinoidea

D. Keith Serafy and F. Julian Fell

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This NMFS Technical Report is part of the subseries, "Marine Flora and Fauna of the Northeastern United States," which consists of original, illustrated, modern manuals on the identification, classification, and general biology of the estuarine and coastal marine plants and animals of the northeastern United States. The manuals are published at irregular intervals on as many taxa of the region as there are specialists available to collaborate in their preparation.

Geographic coverage of the "Marine Flora and Fauna of the Northeastern United States" is planned to include organisms from the headwaters of estuaries seaward to approximately the 200 m depth on the continental shelf from Maine to Virginia, but may vary somewhat with each major taxon and the interests of collaborators. Whenever possible, representative specimens dealt with in the manuals are deposited in the reference collections of major museums of the region.

The "Marine Flora and Fauna of the Northeastern United States" is being prepared in collaboration with systematic specialists in the United States and abroad. Each manual is based primarily on recent and ongoing revisionary systematic research and a fresh examination of the plants and animals. Each manual, treating a separate major taxon, includes an introduction, illustrated glossary, uniform originally illustrated keys, annotated checklist (with information, when available, on distribution, habitat, life history, and related biology), references to the major literature of the group, and a systematic index.

These manuals are intended for use by students, biologists, biological oceanographers, informed laymen, and others wishing to identify coastal organisms for this region. They can often serve as guides to additional information about species or groups.

The manuals are an outgrowth of the widely used "Keys to Marine Invertebrates of the Woods Hole Region," edited by R. I. Smith, and produced in 1964 under the auspices of the Systematics Ecology Program, Marine Biological Laboratory, Woods Hole, MA. After a sufficient number of manuals of related taxonomic groups have been published, the manuals will be revised, grouped, and issued as special volumes, which will consist of compilations for phyla or groups of phyla.

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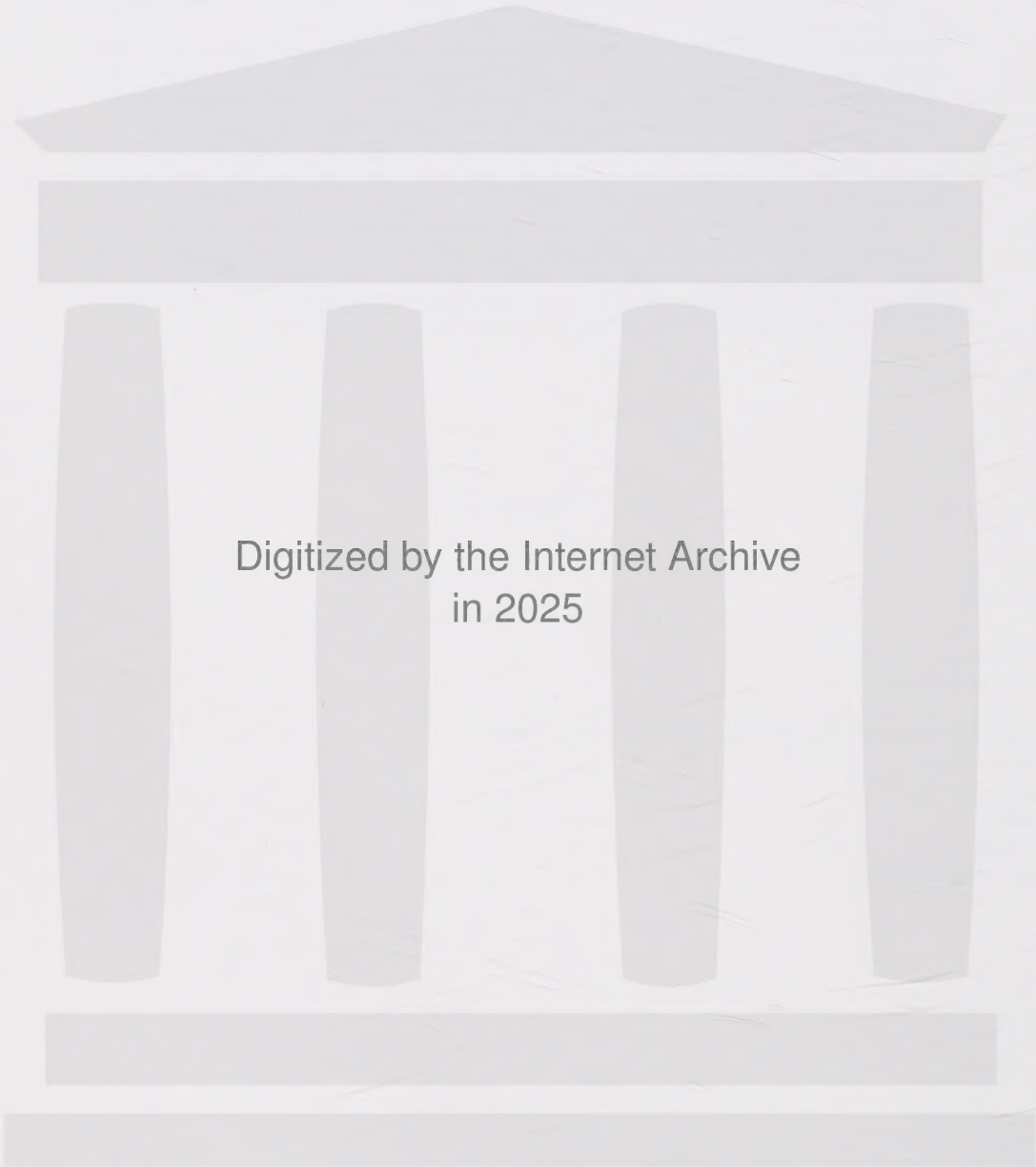

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Marine Flora and Fauna of the Northeastern United States. Echinodermata: Echinoidea

D. KEITH SERAFY[1] and F. JULIAN FELL[2]

ABSTRACT

The echinoid fauna from littoral to abyssal depths off the northeastern United States (Cape Hatteras, NC, to northern Nova Scotia) comprises 31 species, in 26 genera and 19 families. An introduction to the external morphology, distribution, and natural history is given along with an illustrated key to the species, an annotated systematic list, and an index. The fauna includes 17 species with wide-ranging distributions on continental slopes or abyssal plains. The remaining 14 species occur in shallower waters on the continental shelf or upper slope. Of these, eight are tropical in distribution with their northern range extending to the northeastern United States and three are mainly boreal with the northeastern United States at the southern limit of their range. Two species occur only off the eastern United States and one species is cosmopolitan.

INTRODUCTION

The Echinoidea comprise sea urchins, sand dollars, and heart urchins. They are echinoderms with the radial canals of the water vascular system arranged meridionally, and a skeleton composed of fused plates (except in the Echinothurioida). Echinoids have either a pentamerous radial symmetry (regular urchins) or a bilateral symmetry imposed upon the radial pattern (irregular urchins).

The Echinoidea have a relatively stable nomenclature as a result of the work of several dedicated specialists over the last 120 yr. Only a small number of new species are described each year. There are approximately 955 extant species worldwide; 156 are known from the North Atlantic. Echinoids occur from the intertidal to the abyss in all seas. This manual covers the echinoids which occur in North American seas between Cape Hatteras, NC, and northern Nova Scotia at all depths. The number of nominal fossil species is several times greater than the number of extant ones.

EXTERNAL MORPHOLOGY

The rigid calcareous skeleton of echinoids makes it possible to collect most species intact and accounts for their prevalence as fossils. The classification of echinoids is based mostly upon external skeletal features. The skeleton is an endoskeleton composed of calcium carbonate in the form of calcite, which includes about 4-12% magnesium carbonate. The skeletal material is not solid, but is rather a porous matrix. Its internal space is about 50% by volume and contains mesenchymal cells. The shell, or test, is essentially a hollow ball composed of 20 vertical columns of plates, rigidly attached to each other in most species (Fig. 1A-B). There are five ambulacra corresponding to the position of the internal radial water vessels, and each ambulacrum is formed by two vertical columns of plates through which extend the tube-feet. Five interambulacra alternate with the five ambulacra and these also consist of two vertical columns of plates. Sutures mark the adjoining margins of the plates with a faint line or groove.

The lower ends of the columns do not meet at a point, but stop short, leaving a circular hole on the lower (oral) surface of the test. This hole is covered by a membrane called the buccal membrane or peristome in the center of which is located the mouth. In the orders Cidaroida and Echinothurioida, unfused ambulacral plates cross the peristome to the mouth, and each bears a tube-foot. In other regular urchins buccal tube-feet, specialized for feeding, are arranged in a circle around the mouth, one pair to each ambulacrum. In regular echinoids (except Cidaroida) outpocketings of the coelom form five pairs of compensation sacs (gills) which protrude from peristomal notches.

Five teeth protrude through the mouth; these are mounted in a complex jaw structure called Aristotle's lantern. The lantern has proved to be evolutionarily conservative making it an important feature in classification above family level in those groups that possess one.

Test shape is characterized by a number of terms such as low, globular, conical, hemispherical, arched, and others. Descriptions of echinoids usually include a statement on the shape of the test, but this character should never be used alone to key out a species as it can vary even within a species.

Each ambulacrum terminates adapically in a single ocular plate, and each interambulacrum terminates in a single genital plate. The ring of five ocular plates alternating with the five genital plates form the apical system (Fig. 1C). In regular urchins the periproct and anus are within the apical system. Each genital plate has a genital pore for the discharge of eggs or sperm. One of the genital plates functions as the madreporite or sieve plate and is usually enlarged and covered with small pores.

Each ambulacral plate carries one tube-foot which may vary considerably in form and function. Tube-feet can function in respiration, locomotion, reception of stimuli, burrowing, feeding, or any combination of these. Each tube-foot connects to the radial canals within the test by a pair of adjacent pores. Simple ambulacral plates (Fig. 2A) have one pore-pair and occur in the cidaroids and all the irregular echinoids. Compound ambulacral plates (Figs. 2B-F) have 2 to 16 pore-pairs since they are formed by the fusion of 2 to 16 simple plates. Most regular echinoids have compounded ambulacral plates which enable the tube-feet to be concentrated in certain areas (e.g., near the mouth). Compounded ambulacral plates are also capable of bearing larger spines than simple plates.

[1]Department of Biology, Southampton College, Southampton, NY 11968.

[2]Department of Zoology, University of Maine, Orono; present address: 405 Vancouver Street, Victoria, B.C. V8V 3T4, Canada.

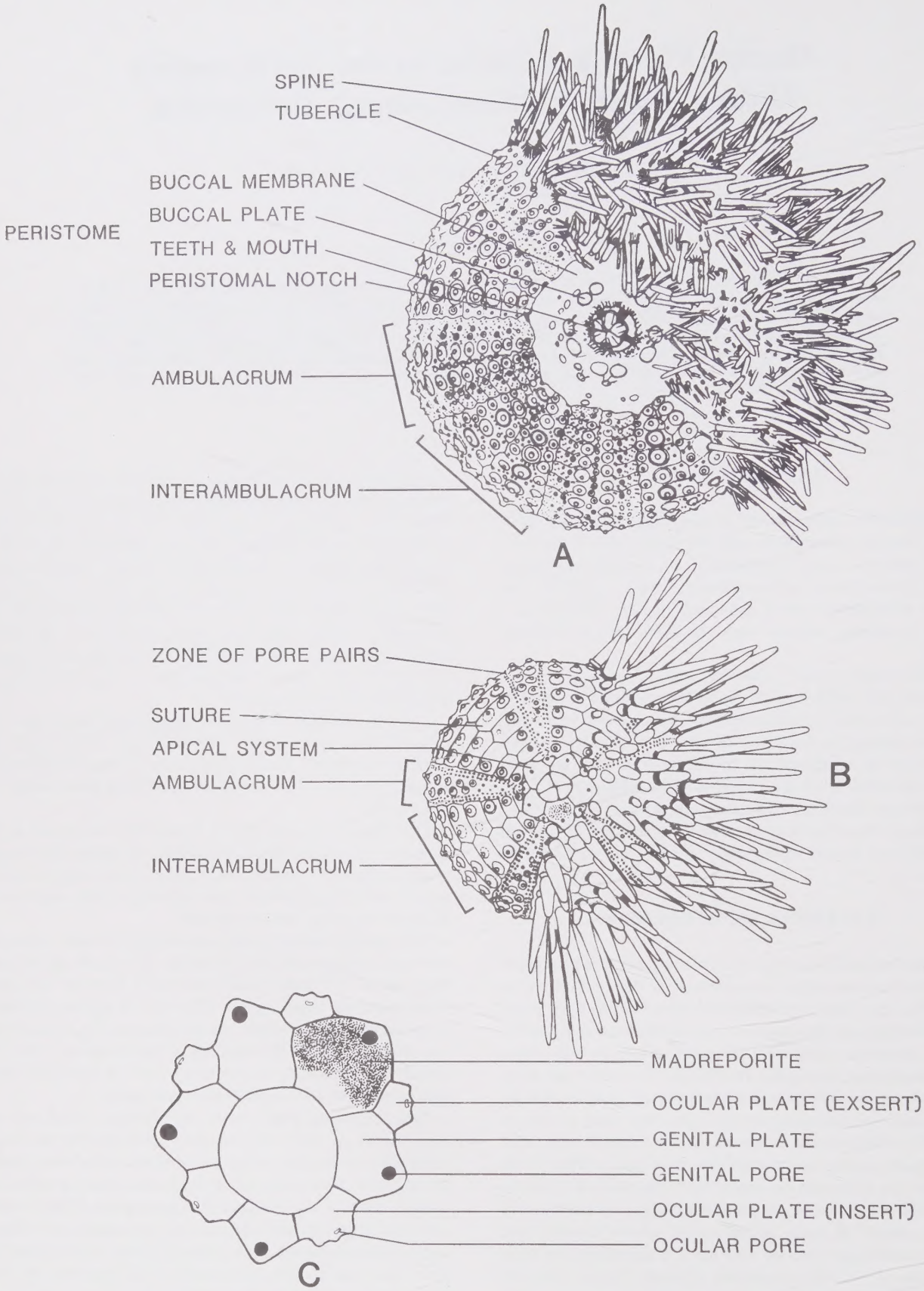

Figure 1.—External features of regular urchins. A, oral surface of *Strongylocentrotus droebachiensis*; B, aboral surface of *Arbacia punctulata*; C, apical system of *S. droebachiensis*.

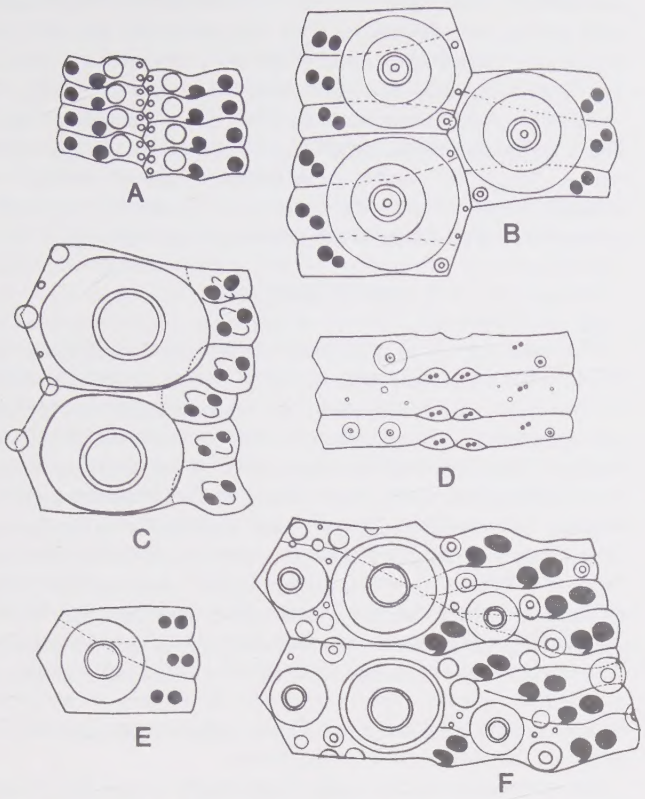

Figure 2.—Ambulacral plates. A, simple plates of the Cidaroida; B, diadematoid type of compound plates (middle plate enlarged) seen in *Caenopedina*; C, arbacioid type of compound plates seen in *Arbacia*; D, echinothurioid type of compound plates seen in *Araeosoma*; E, echinoid type of compound plates (lower plate enlarged) seen in *Echinus*; F, echinoid type of compound plates seen in *Strongylocentrotus*.

There are four forms of compound plates, named for characteristic orders. Diadematoid type compound plates are composed of three primary plates (in contact with adradial and perradial sutures) with the middle one the largest (Fig. 2B). Arbacioid type plates have the middle primary plate so enlarged that the other plates become demiplates, no longer in contact with the perradial suture (Fig. 2C). Echinothurioid type plates are composed of a large primary plate and two small included plates between the primary plates (Fig. 2D). Echinoid type plates have three or more elements with the adoral and adapical plates being primary plates and the remaining ones being demiplates (Fig. 2E-F). The adoral primary plate is always the largest.

Plates of the test bear rounded tubercles which carry the spines. Each tubercle consists of a raised central boss capped by a smooth, shiny, hemispherical mamelon (Fig. 3). The mamelon may have a small hole in the top, in which case it is termed perforate. Mamelons lacking this hole are imperforate. The upper edge of the boss surrounding the mamelon may be indented (crenulate) or smooth (noncrenulate).

Spines vary considerably in form and function. They are used for locomotion, protection from predators and the environment, feeding, and burrowing. In burrowing forms, a dense covering of fine spines keeps sand and mud off the test, essentially surrounding the test in a jacket of water. Spines form a ball-and-socket joint with mamelons and are moved by a ring of radially arranged muscles at the base of the spine. Relatively unspecialized spines may be primary (largest), secondary (small to medium), or miliary (hairlike and usually short) depending on relative size. Other terms are applied to specialized types of spines.

In addition to spines and tube-feet the surface of the test bears many small clasping structures, the pedicellariae. Pedicellariae are of several types and function in defense, feeding, and cleaning. Although useful for classification and identification, they are not included in this manual, for special knowledge and techniques are required for their study.

The irregular (excentric or exocyclic) echinoids (Fig. 4) differ from the regular echinoids in that the periproct is displaced from the apical system into what becomes the posterior interambulacrum. Displacement of the periproct and other modifications impart a conspicuous bilateral symmetry to the irregular echinoids.

Irregular echinoids comprise five distinct orders. Clypeasteroida (sand dollars and cake urchins), Holasteroida (heart urchins), and Spatangoida (heart urchins) include many living species and they are well represented in waters off the northeastern United States. Holectypoida and Cassiduloida are primarily fossil groups with very few living species worldwide; none occur off the northeastern United States.

The morphological differences between regular and irregular echinoids are primarily adaptations to a burrowing existence in sand and mud. The earliest irregular echinoids arose in the Early Jurassic (Sinemurian), and 10 million yr later they had developed all the features necessary to permit them to live infaunally (Kier 1982). Some irregular echinoids live on the surface of the sediments. Adaptations to burrowing include a loss of compensation sacs (gills) on the oral surface and development of petals on the aboral surface which serve in respiration. Spines are smaller and more numerous than in regular echinoids. Aristotle's lantern is absent in the Cassiduloida, Holasteroida, and Spatangoida and food gathering is accomplished with spines or specialized tube-feet. Irregular urchins that do not burrow have rudimentary petals and sparse aboral spine coverage, although the spines may be greatly enlarged.

Clypeasteroida comprise a large group of about 140 extant species, two of which occur off the northeastern United States. In this group five respiratory petals extend from a generally central apical system. Microscopic pores for accessory tube-feet are

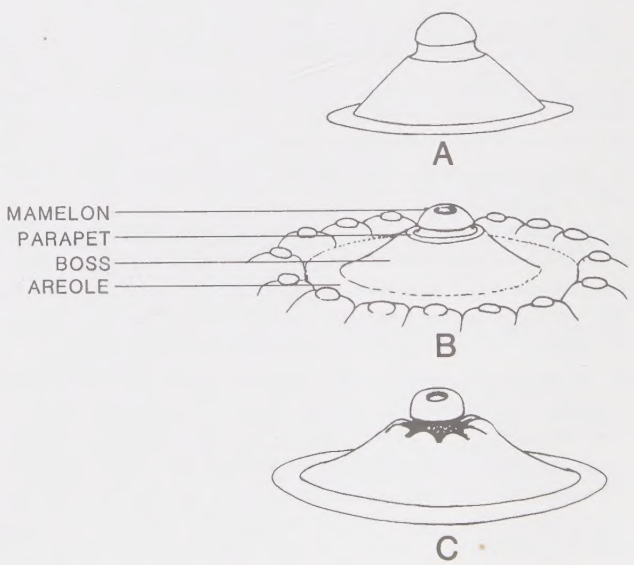

Figure 3.—Types of primary tubercles. A, imperforate; B, perforate; C, perforate and crenulate.

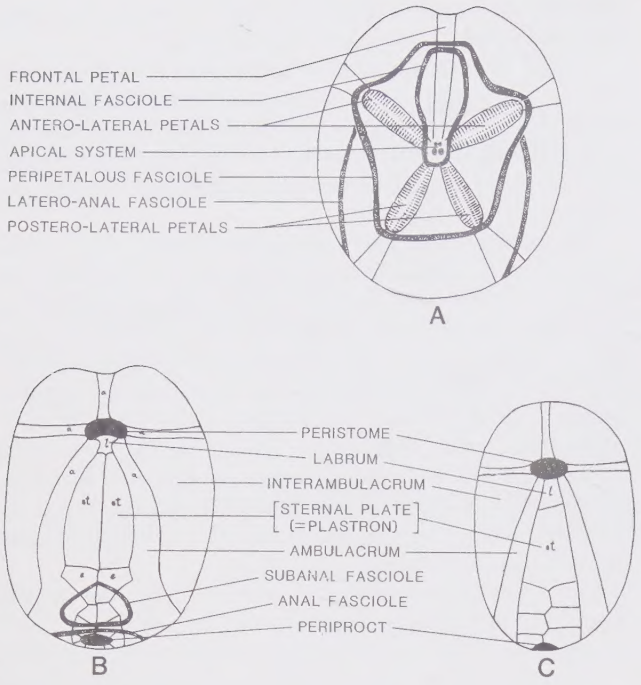

Figure 4.—External features of irregular urchins (Spatangoida and Holasteroida). A, aboral surface; B, oral surface with amphisternous plastron; C, oral surface with meridosternous plastron.

numerous and may occur to varying degrees over the test. Accessory tube-feet are present over wide areas on either side of the ambulacra and they function to pull and hold sand over the test. The mouth is central (opposite the apical system) and an Aristotle's lantern is present. The periproct, located on the oral surface in the posterior interambulacrum, is either near the margin or near the peristome. In some species the test has slits or lunules which are used in burrowing and feeding. Most species have ciliated food grooves on the oral surface; in a few species the grooves extend to the aboral (upper) surface. The test surface is densely covered with small miliary spines. Larger primary spines are relatively few, and several types of pedicellariae are present.

The Holasteroida comprise a small group of heart urchins with a single large plate (meridosternous) comprising the sternum (Fig. 4C). The mouth is situated anteriorly and there is no Aristotle's lantern. The apical system is longitudinally elongated or disjunct and the paired petals are poorly developed or absent. Most species are found only in deep water and three species occur off the northeastern United States.

The Spatangoida comprise a large group of about 200 species, of which 8 occur off the northeastern United States. The mouth is situated anteriorly and there is no Aristotle's lantern. The first plate of the posterior interambulacrum forms a liplike structure, the labrum, which projects forward under the mouth. Posterior to the labrum is the plastron which consists of two (amphisternous) enlarged, interambulacral plates (Fig. 4B). The periproct is situated posteriorly, usually where the test surface is vertical. Petals are present but not all are of uniform size or development. Whatever the condition of the petals, they are always bilaterally symmetrical. The tube-feet are adapted for respiration in the paired petals, for tunnel building and maintenance in the anterior ambulacrum and around the periproct, and for feeding around the mouth. The apical system may be situated posteriorly, centrally, or anteriorly. The shapes of spines vary considerably according to their position on the test, although adaptations are generally for burrowing. Burrowing is assisted by waves of spine movements that begin anteriorly and move posteriorly. Minute spines, or clavules, have cilia along the shaft and a mucus gland on the end. These are specialized for circulating water over the surface of the test and lining the burrows with mucus. Tracts of clavules, or fascioles, follow characteristic paths over the surface of the test and are named according to the positions they occupy (Fig. 4).

DISTRIBUTION

With the exception of shallow-water species endemic to isolated mid-oceanic islands, echinoid species characteristically are distributed over large geographic and bathymetric ranges. The majority of species live on the outer continental shelf and slope in depths > 50 m. *Cidaris*, *Genocidaris*, and *Plethotaenia* are endemic to the North Atlantic. *Stereocidaris*, *Araeosoma*, *Hygrosoma*, *Phormosoma*, *Caenopedina*, *Plesiodiadema*, *Salenocidaris*, *Urechinus*, *Plexechinus*, *Pourtalesia*, *Hemiaster*, *Aeropsis*, *Aceste*, *Schizaster*, *Brisaster*, *Brissopsis*, and *Echinocardium* have worldwide, moderate to deep-water distributions. The Arbaciidae and Mellitidae are of tropical American origin. Both *Strongylocentrotus* and *Echinarachnius* occur in the North Atlantic and North Pacific.

Only three species, *Arbacia punctulata*, *Strongylocentrotus droebachiensis*, and *Echinarachnius parma*, are common in shallow water off the northeastern United States.

The echinoid fauna from Cape Hatteras, NC, to northern Nova Scotia comprises 31 species in 26 genera and 19 families. It includes species which are known to occur or are considered likely to occur in the study area from the littoral to the deep abyss. The largest component of the fauna (17 species) consists of deep-water forms which occur on the continental slope or abyssal plain over wide ranges of latitude and often on both sides of the Atlantic Ocean. These species include *Stereocidaris ingolfiana*, *Araeosoma fenestratum*, *Hygrosoma petersi*, *Phormosoma placenta*, *Plesiodiadema antillarum*, *Caenopedina cubensis*, *Salenocidaris variaspina*, *Salenocidaris profundi*, *Echinus affinis*, *Echinus alexandri*, *Urechinus naresianus*, *Plexechinus hirsutus*, *Pourtalesia miranda*, *Hemiaster expergitus*, *Aeropsis rostrata*, *Aceste bellidifera*, and *Brissopsis mediterranea*. The remaining 14 species occur in shallow to moderate depths on the continental shelf or upper slope. Eight of these species (*Cidaris abyssicola*, *Coelopleurus floridanus*, *Arbacia punctulata*, *Genocidaris maculata*, *Echinus gracilis*, *Mellita quinquiesperforata*, *Schizaster orbignyanus*, and *Plethotaenia spatangoides*) are mostly tropical in distribution and are at or near the northern limits of their range in the study area. Three species (*Strongylocentrotus droebachiensis*, *Echinarachnius parma*, and *Brisaster fragilis*) are mostly Arctic-Boreal in distribution and are at or near the southern limits of their range off the northeastern United States. Two species occur only off the eastern United States (*Echinus tylodes* and *Echinus wallisi*) while one species is cosmopolitan (*Echinocardium cordatum*) in distribution.

NATURAL HISTORY

Little is known of the natural history of most echinoids, particularly deep-water species. However, it is possible to predict the life styles of many species (epifaunal, infaunal) from their morphology and habitat. Regular echinoids are epifaunal on hard or soft substrates and most shallow-water species (< 50 m) feed on algae or seagrasses. Deep-water forms are more omnivorous and usually ingest sediments, small invertebrates, or plant fragments

that have been transported from shallower depths. Most irregular echinoids are infaunal and burrow through the sediments, although some species (sand dollars and a few heart urchins) remain epifaunal most of the time. Most species are either surface deposit feeders ingesting organic-rich detritus, or are subsurface feeders ingesting sediments as they burrow. Lawrence (1975) gave an excellent review of feeding in echinoids.

Sexes are separate, and most species shed eggs or sperm into the water where fertilization occurs. Most species have a planktotrophic echinopleuteus larva. The larva eventually metamorphoses to form a young echinoid. A few species have direct development and even fewer brood their young. Sexually ripe individuals can usually be induced to spawn in the laboratory by injection of 3% KCl solution through the peristome into the coelom. Electrical shock to the peristome may also induce spawning.

Echinoids may be kept alive in aquaria for extended periods of time if the water is kept clean and is of the appropriate salinity and temperature for the species. Cold-water species must be maintained in refrigerated aquaria. Most shallow-water regular echinoids can be fed a variety of algae although they may show distinct preferences. Large individuals may occasionally eat smaller specimens kept in the same aquarium. Irregular echinoids are more difficult to maintain and they should be provided with the appropriate sediments from their habitats.

PRESERVATION AND EXAMINATION

Echinoids may be fixed and preserved in 10% Formalin or 70% ethyl alcohol. Specimens in Formalin are best transferred to alcohol after 1-3 d. After fixation in preservative, echinoids may be dried. This is the most convenient condition for study and storage. Colors tend to fade upon preservation, especially if alcohol is used.

A small portion of the test can be cleaned to observe surface details. Spines on an ambulacral and interambulacral area can be removed by hand or with a brush, and organic tissue can be removed without damage to the skeletal calcite by immersion in a 5% sodium hypochlorite solution (i.e., commercial liquid bleach) for a few minutes. Calcite may be removed from the soft tissue by immersion for a week in 3-5% acetic acid. Sutures between the plates are easy to observe if xylene is applied to a dried specimen with a small paint brush.

GLOSSARY

Aboral Away from the mouth.

Accessory tube-feet Small tube-feet found in ambulacral and interambulacral areas of the Clypeasteroida.

Adapical Towards the apical system.

Adoral Towards the mouth.

Adradial Boundary between ambulacral and interambulacral areas.

Ambulacrum Area of test corresponding to position of radial water vessel and consisting of two regular vertical columns of plates. Five ambulacra alternate with five interambulacra.

Amphisternous Plastron of paired plates.

Anus Opening of intestine located within periproct.

Apical system Circle of alternating genital and ocular plates at aboral pole of test.

Arbacioid type Compound ambulacral plate composed of three primary plates in which the middle plate is so enlarged that the adapical and adoral plates are demiplates.

Aristotle's lantern Complex dental apparatus at mouth.

Boss Basal part of raised portion of tubercle.

Buccal membrane Peristome. Covering of aperture at oral pole of test.

Buccal tube-feet Tube-feet on peristome usually occurring in single circle of five pairs corresponding to radial position.

Clavules Minute spines with cilia on shaft and mucus gland at tip. These tightly packed spines occur in lines on the surface of the test known as fascioles.

Compensation sac Outpouching of coelom often called "gills" but which function primarily to receive excess coelomic fluid from retraction of Aristotle's lantern.

Compound plate Ambulacral plate composed of fused plates.

Crenulate Upper edge of boss notched or scalloped.

Demiplate Ambulacral plate which touches adradial suture but not perradial suture.

Diadematoid type Compound ambulacral plate in the order Diadematoida where the middle of three primary plates is expanded perradially and adradially.

Echinoid type Compound ambulacral plate in the order Echinoida, where lowest demiplate is the largest.

Echinothurioid type Compound ambulacral plate with a single large primary plate with two small included plates located between the primary plates.

Exocyclic Periproct located outside of the apical system.

Fascioles Tracts of crowded clavules for circulating water over surface of test in spatangoid urchins.

Food grooves Spine-free ciliated grooves on lower surface of sand dollar radiating from mouth.

Genital plate Single plate at aboral end of each interambulacral area.

Genital pore Pore on each genital plate for shedding gametes.

Imperforate tubercle Mamelon of tubercule without central hole.

Interambulacrum Area of test corresponding to interradial position, consisting of two regular vertical columns of plates. Five interambulacra alternate with five ambulacra.

Irregular Informal term for all taxa in which periproct has moved from within apical system disrupting radial symmetry, and conferring conspicuous bilateral symmetry.

Labrum First plate at edge of mouth of posterior interambulacrum in spatangoid urchins.

Lunules Holes or notches in mid-ambulacral or mid-interambulacral areas of sand dollars.

Madreporite Enlarged porous genital plate connecting to water-vascular system.

Mamelon Smooth raised hemisphere forming central and highest part of tubercle.

Meridosternous Plastron of single plate.

Miliary Very small spines on Cidaroida and Clypeasteroida.

Noncrenulate Upper edge of boss not scalloped (smooth).

Ocular plate Single plate at terminus or radial canal located at aboral end of each ambulacrum.

Oculo-genital ring Apical system.

Pedicellariae Small, 2-4 jawed, stalked, clasping structures on surface of test.

Perforate tubercle Hole in center of mamelon of tubercle.

Periproct Membrane-covered aperture which includes the anus, located at aboral pole or in posterior interambulacrum.

Peristomal notch Notch for compensation sac located along margin of periproct.

Peristome Buccal membrane. Covering of aperture at oral pole of test.

Perradial Having meridional position at midline of ambulacrum.

Petals Structures of aboral ambulacra in which many simple

plates are widened laterally, compressed and crowded longitudinally. Found mostly on burrowing irregular echinoids.

Plastron Shield of enlarged plates of posterior interambulacrum following labrum on lower surface of spatangoid urchins.

Pore-pair Two adjacent pores on ambulacral plates passing through the test providing passage between tube-feet outside and radial canal inside.

Regular Informal term for all taxa in which periproct is located within apical system, retaining radial symmetry.

Sieve plate Madreporite.

Simple plate Ambulacral plate uncompounded, bearing single pore-pair.

Spine Movable elongated calcareous shaft mounted on tubercle and articulating with it.

Suranal plate First-formed and largest plate of periproctal system.

Suture Adjoining margins of test plates usually marked by faint line or groove.

Test Hollow shell composed of 20 regular vertical columns of plates forming basic skeleton of echinoids.

Tube-feet Part of water-vascular system running from radial canal, passing through test in the ambulacra and extending into surrounding water, usually terminating with a sucker.

Tubercle Specialized structure on test surface for supporting spine; includes raised and surrounding flat or recessed parts.

KEY TO THE ECHINOIDEA FROM ALL DEPTHS OFF THE NORTHEASTERN UNITED STATES

1 Test flattened, disc-shaped, height 25% or less of diameter 2

1 Test subglobular to globular, height 40-100% of diameter 3

2 (*1*) Test rigid. Spines uniformly small, numerous, forming dense covering. Tubercles minute. Petals present. Margin acute 21

2 (*1*) Test flexible. Primary spines and tubercles present. No petals. Margin rounded 9

3 (*1*) Test radially symmetrical, circumference approximately circular or slightly pentagonal. Largest spines in distinct vertical rows. Mouth in center of lower side, teeth (lantern) present. Anus in center of upper surface (Figs. 1, 5) 4

3 (*1*) Test bilaterally symmetrical, slightly to strongly ovoid. Spines numerous, forming dense uniform covering with petals present, or few spines and no petals. Mouth towards "anterior" end, teeth (lantern) lacking. Anus in "posterior" interambulacrum. On lower surface behind mouth posterior interambulacrum modified into shieldlike plastron (Figs. 4, 6) 22

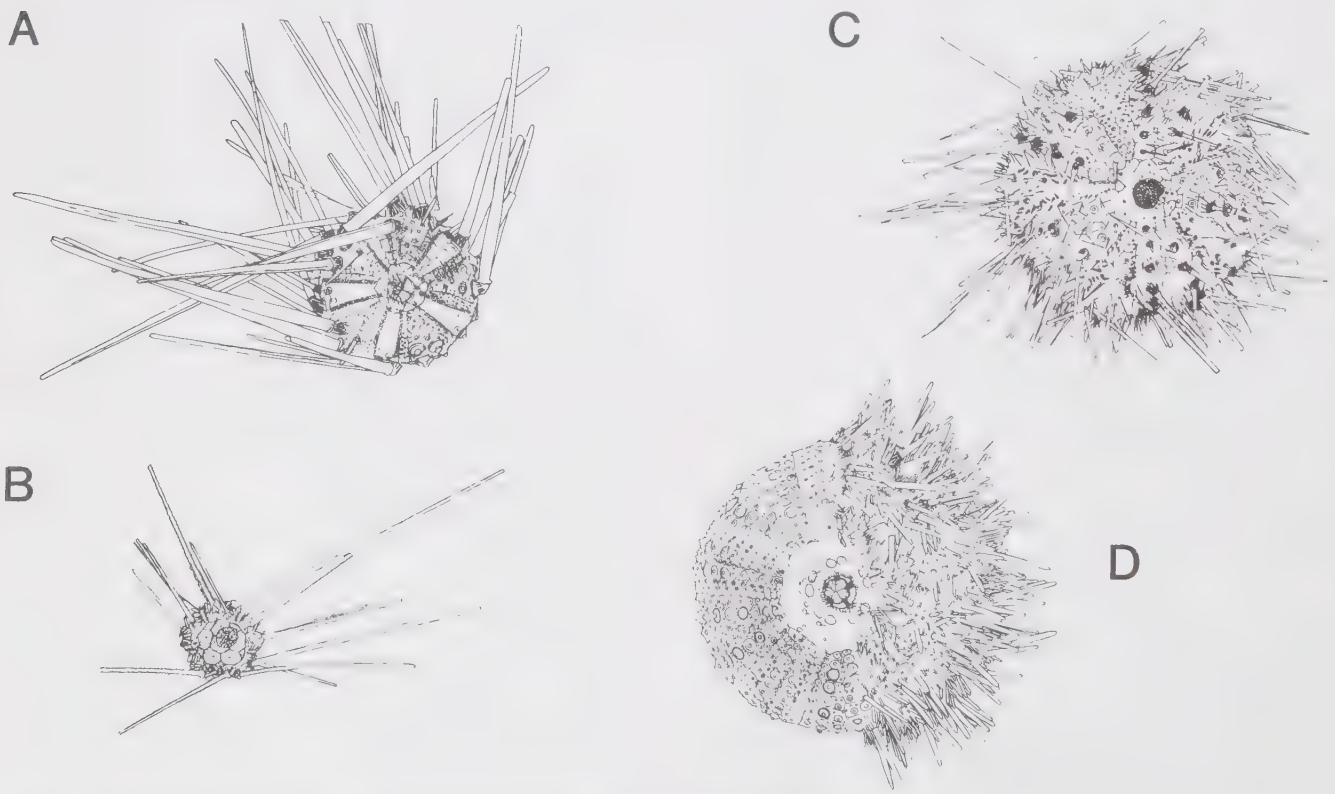

Figure 5.—Examples of regular urchins. A, *Coelopleurus* (aboral aspect); B, *Salenocidaris* (aboral aspect); C, *Echinus* (aboral aspect); D, *Strongylocentrotus* (oral aspect).

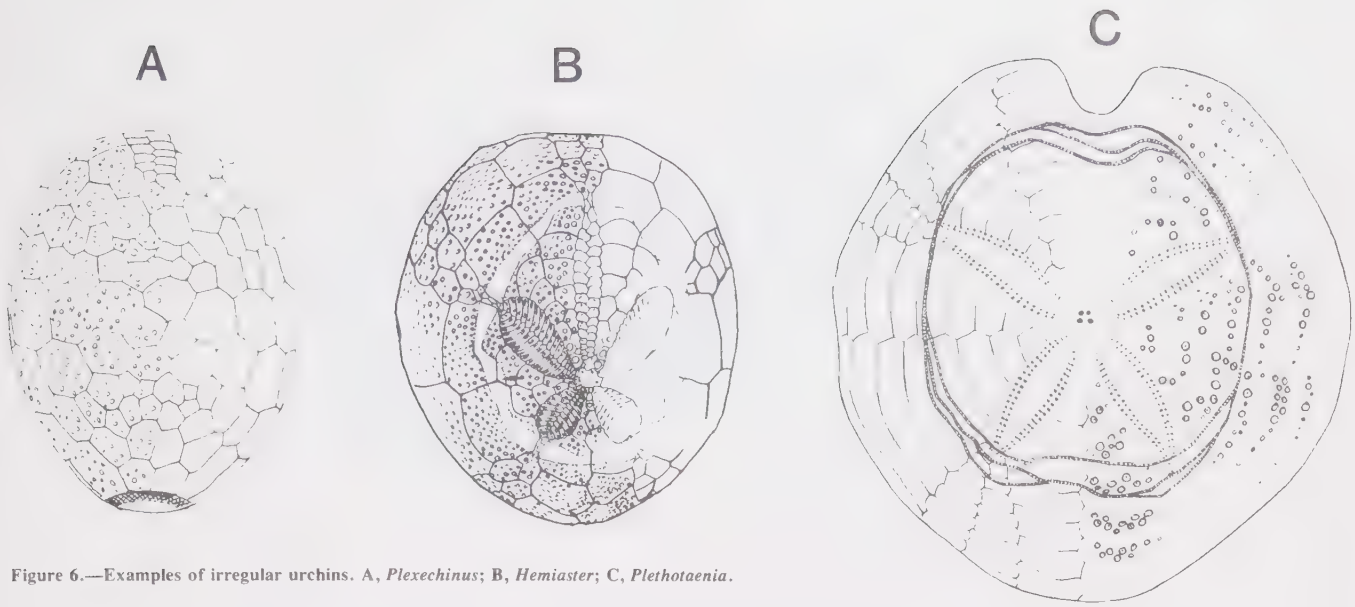

Figure 6.—Examples of irregular urchins. A, *Plexechinus*; B, *Hemiaster*; C, *Plethotaenia*.

4 (*3*) Tubercles perforate (Fig. 7) 5

4 (*3*) Tubercles imperforate (Fig. 8) 11

5 (*4*) Test rigid, height exceeding 40% of diameter. Each interambulacral plate with one primary tubercle 6

5 (*4*) Test flexible, usually collapsed to a disc upon preservation. Primary tubercles on lower side numerous, reduced or absent from upper surface (usually >200 m) 9

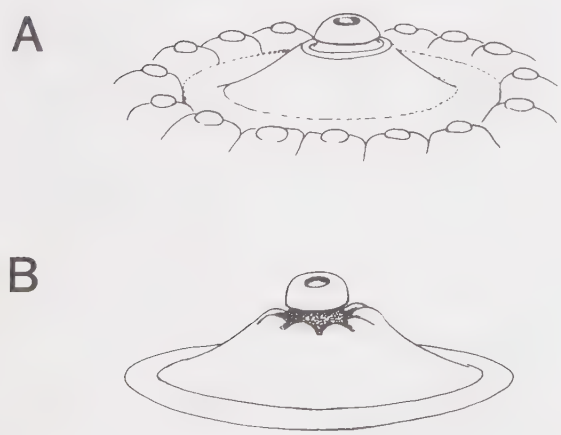

Figure 7.—Perforate primary tubercles. A, crenulate; B, noncrenulate.

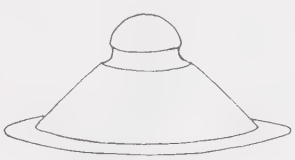

Figure 8.—Imperforate primary tubercle.

6 (5) Spines hollow, very long, slender, and fragile. Tubercles crenulate. Ambulacral plates simple, grouped in triads. Color light purple. Test to 15 mm diameter, spines to 120 mm (Fig. 9) ..... *Plesiodiadema antillarum*

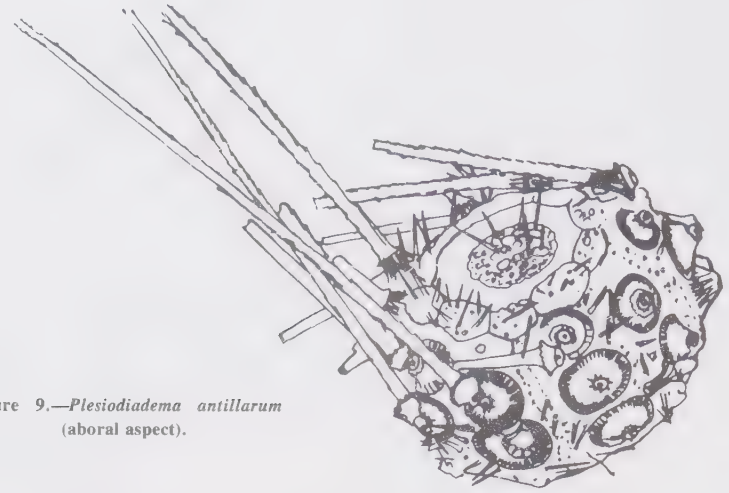

Figure 9.—*Plesiodiadema antillarum* (aboral aspect).

6 (5) Spines solid, robust. Tubercles not crenulate 7

7 (6) Ambulacral plates simple (Fig. 10A) continuing across peristome. Interambulacral plates large (Fig. 10B), few, each with single primary tubercle and spine 8

7 (6) Ambulacral plates compounded with 3 pore-pairs per plate in diadematoid type (Figs. 2B, 11). Peristome with 5 pairs of buccal plates, otherwise naked. Primary spines of adults long and tapered. Spines pale green, test whitish. Test to 40 mm diameter ..... *Caenopedina cubensis*

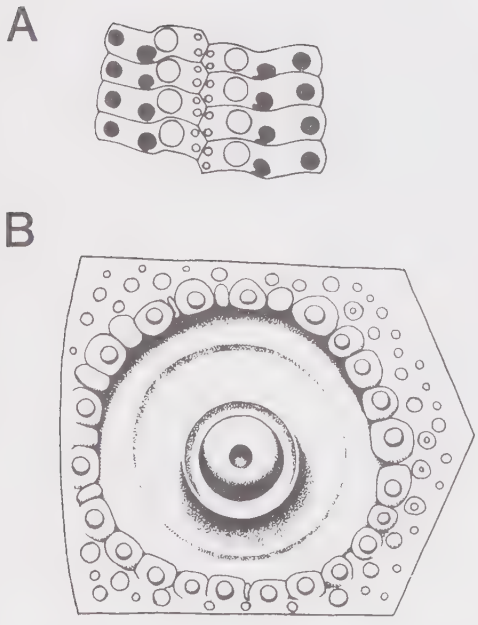

Figure 10.—Test plates in the Cidaroida. A, simple ambulacral plates; B, interambulacral plate.

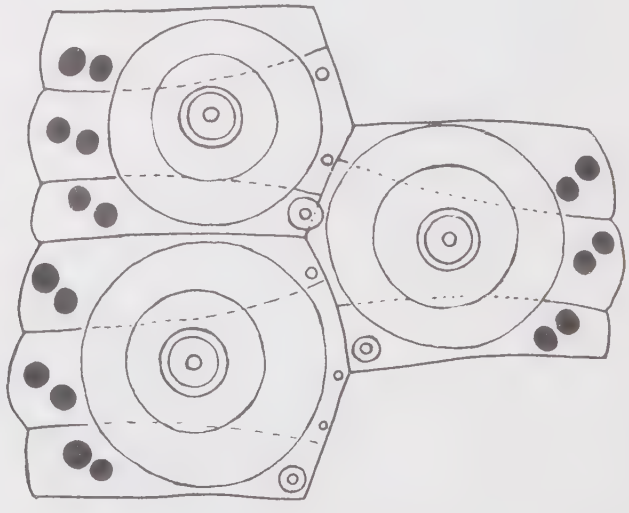

Figure 11.—Diadematoid type compound ambulacral plates of *Caenopedina cubensis*.

8 (7) Primary spines smooth and shiny on adults, although smaller specimens may have small spinules. Scrobicular and secondary spines flattened and broader at base than at tip. Test generally whitish, may have brown tint at apical system and on vertical sutures. Test to 70 mm diameter (Fig. 12) ..... *Cidaris abyssicola*

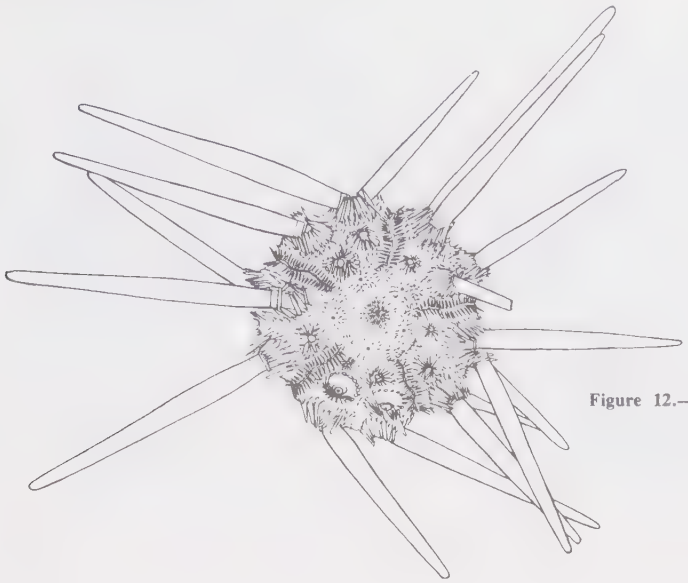

Figure 12.—*Cidaris abyssicola* (aboral aspect).

8 (7) Primary spines covered with spinules and in large adults they may be "winged" with raised flutes. Scrobicular spines flattened and broader at base than at tip but secondary spines very tiny and not broader at base than at tip. Test generally tan to whitish, spines pinkish. Test to 25 mm diameter (Fig. 13) ..... *Stereocidaris ingolfiana*

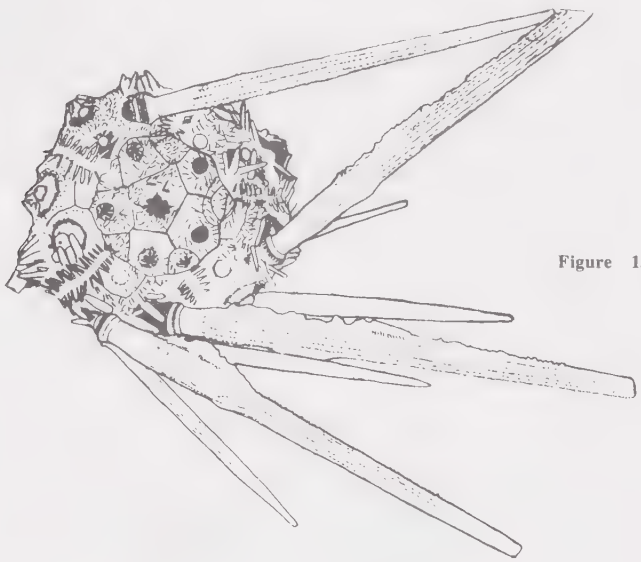

Figure 13.—*Stereocidaris ingolfiana* (aboral aspect).

9 (2, 5) Compound ambulacral plates on aboral surface of echinothurioid type with two very small included plates lying between the primary plates (Fig. 14) 10

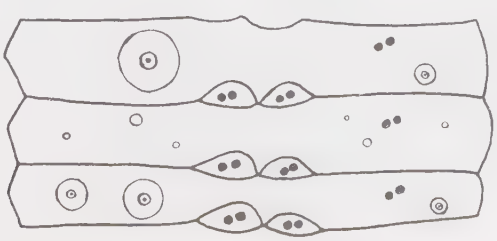

Figure 14.—Echinothurioid type compound ambulacral plates.

9 (2, 5) Compound ambulacral plates of oral and aboral surface of arbacioid type (Fig. 15C). Test flat below, slightly arched above. Oral side (Fig. 15A) covered with primary tubercles bearing long, club-shaped spines enclosed in membranous sacs. Aboral surface (Fig. 15B) relatively bare. Color yellowish to brown. Test to 120 mm diameter . . . *Phormosoma placenta*

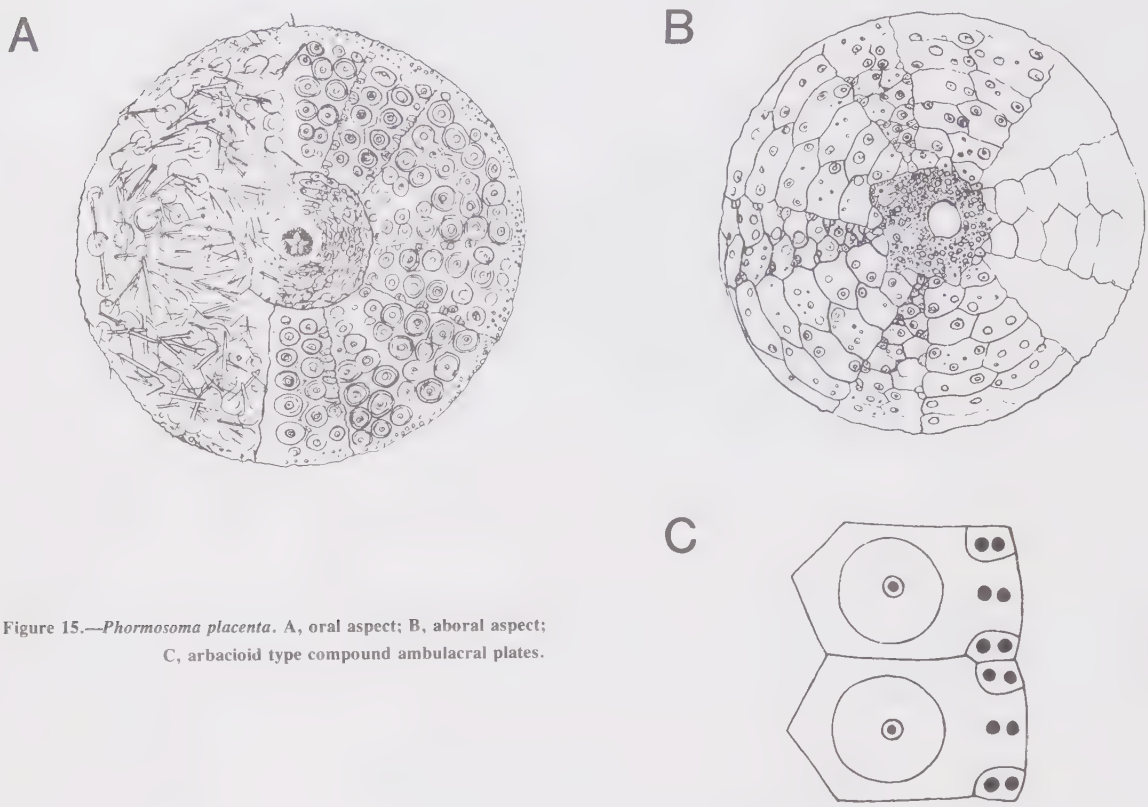

Figure 15.—*Phormosoma placenta*. A, oral aspect; B, aboral aspect; C, arbacioid type compound ambulacral plates.

10 (9) Echinothurioid type compound ambulacral plates on oral and aboral surface (Fig. 16). Each oral primary spine tipped with small white shiny hoof. Interambulacral plates with conspicuous membranous interstices along horizontal sutures. Color brownish with a trace of purple. Test to 200 mm diameter . . . . . *Araeosoma fenestratum*

10 (9) Echinothurioid type compound ambulacral plates on aboral surface (Fig. 17A) and arbacioid type compound ambulacral plates on the oral surface (Fig. 17B). Each primary spine on oral side tipped with large white hoof (most are broken off in preserved specimens). Interambulacral plates without membranous interstices. Color bright purple. Test to 200 mm diameter . . . . . *Hygrosoma petersi*

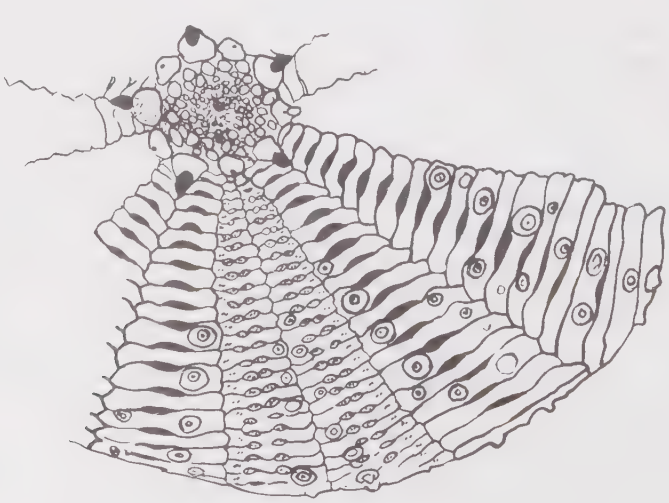

Figure 16.—*Araeosoma fenestratum* (aboral aspect).

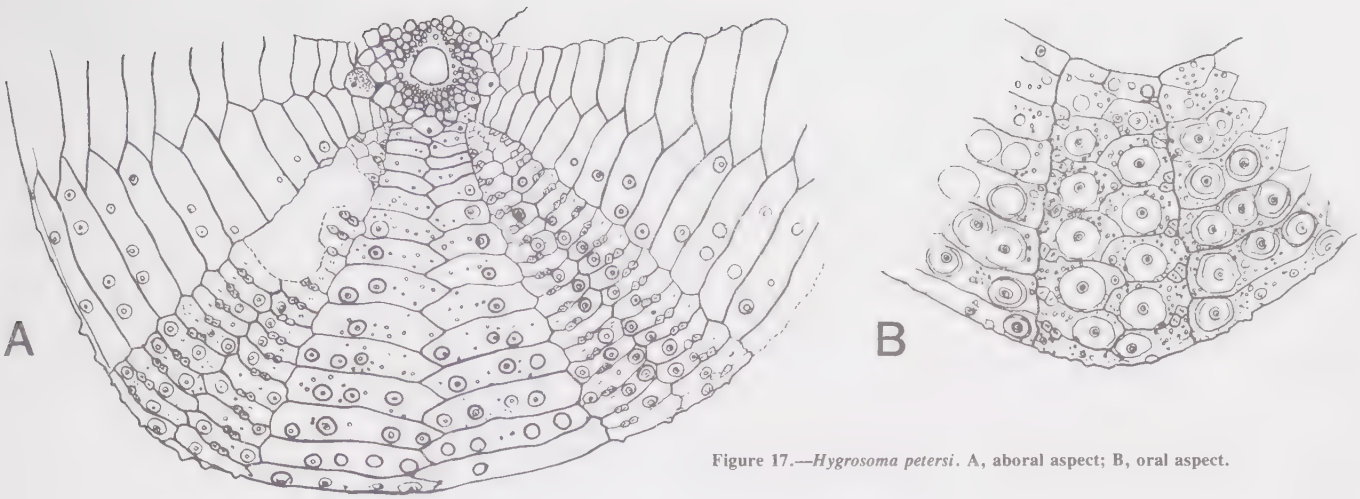

Figure 17.—*Hygrosoma petersi*. **A, aboral aspect; B, oral aspect.**

11 (*4*) Apical system large, periproct off-center due to suranal plate. Tubercles crenulate. Spines white, shiny, long and slender, sometimes thorny. Interambulacral plates few, each with single, large, primary tubercle. Ambulacral plates simple except near the peristome where they are compounded in two's. Genus *Salenocidaris* (Fig. 18) 12

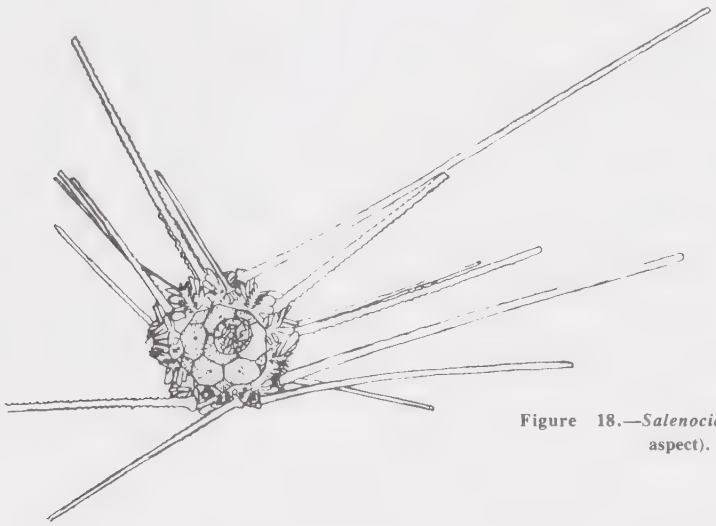

Figure 18.—*Salenocidaris* **(aboral aspect).**

11 (*4*) Periproct central. Tubercles noncrenulate. Spines smooth. Ambulacra with 3 or more pore-pairs per compound plate 13

12 (*11*) Test white, periproct purple. Spines on periproct short, enlarged distally, sometimes almost globular (Fig. 19). Test to 12 mm diameter, spines 30-45 mm length ..... *Salenocidaris varispina*

Figure 19.—**Periproctal spine of** *Salenocidaris varispina*.

12 (*11*) Whitish all over. Spines on periproct tapered distally (Fig. 20). Test to 16 mm diameter, spines 40-60 mm length ..... *Salenocidaris profundi*

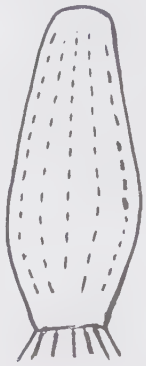

Figure 20.—Periproctal spine of *Salenocidaris profundi*.

13 (*11*) Echinoid type compound ambulacral plates with 5-7 pore-pairs per plate (Fig. 21A). Test height 50-65% diameter, arched. Test covered with spines and tubercles, no naked areas. Primary tubercles and spines forming distinct vertical series but not much larger than secondaries. Color green with different degrees of red-brown. Spines may be whitish. Test up to 100 mm diameter, 60 mm usual maximum (Fig. 21B) ..... *Strongylocentrotus droebachiensis*

13 (*11*) Ambulacral plates compounded with 3 pore-pairs per plate (either arbacioid or echinoid type) 14

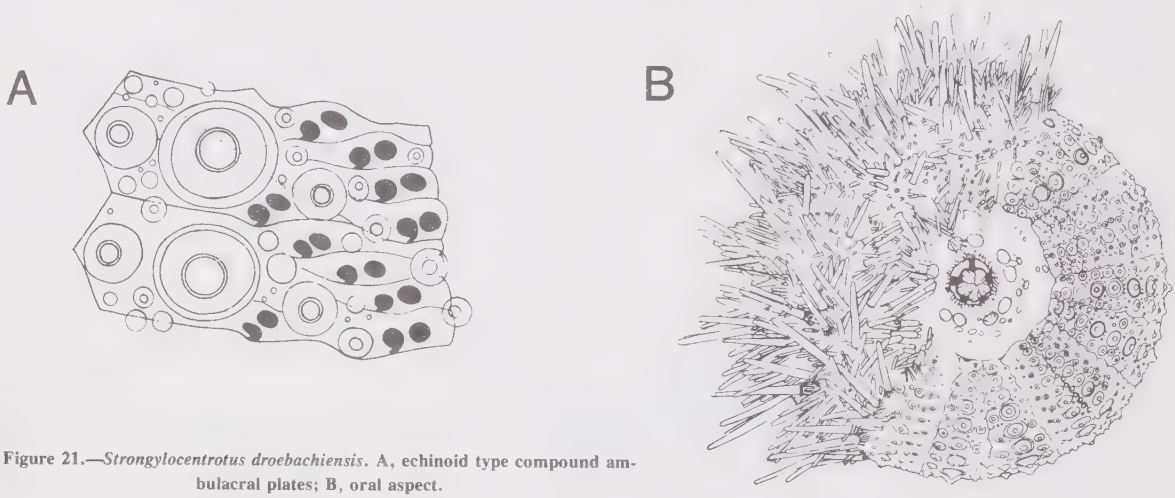

Figure 21.—*Strongylocentrotus droebachiensis*. A, echinoid type compound ambulacral plates; B, oral aspect.

14 (*13*) Periproct covered by 4 triangular plates (Fig. 22A) simulating anal pyramid. Arbacioid type compound ambulacral plates (Fig. 22B). Mid-interambulacral areas on upper surface naked. Secondary spines absent or poorly developed. Family Arbaciidae 15

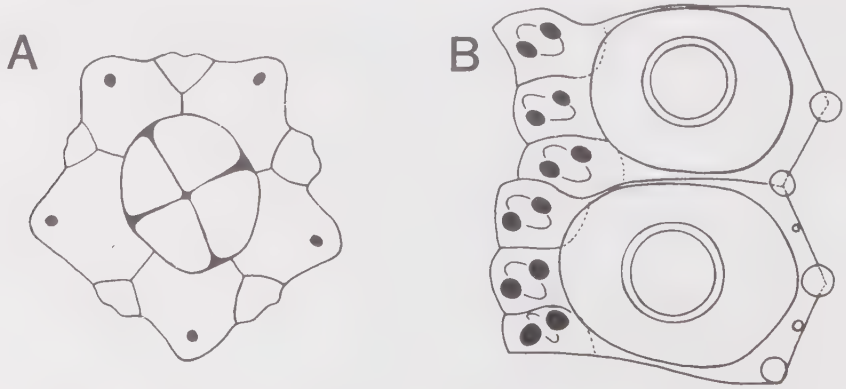

Figure 22.—Arbaciidae features. A, apical system; B, arbacioid type compound ambulacral plates.

14 (*13*) No triangular periproctal plates, mid-interambulacral areas tuberculated. Echinoid type compound ambulacral plates 16

15 (*14*) Test hemispherical to subconical. Spines circular in cross section. Secondary spines absent. Test and spines uniform brown, deep red, purple, or black. Test to 56 mm diameter (Fig. 23) . . . . . *Arbacia punctulata*

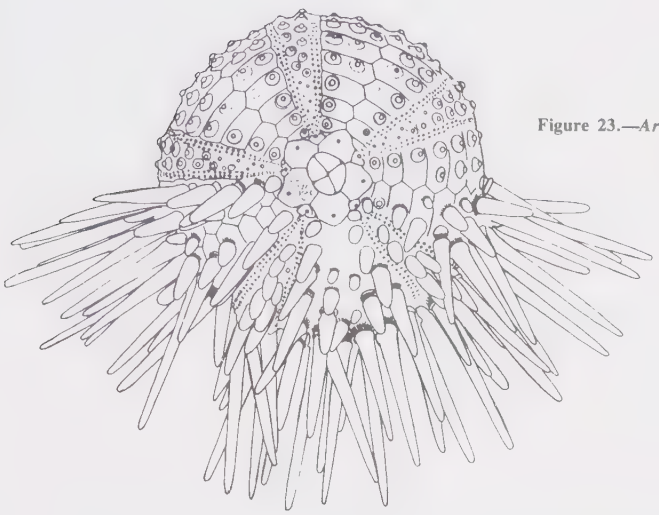

Figure 23.—*Arbacia punctulata* (aboral aspect).

15 (*14*) Test slightly pentagonal, hemispherical to subconical. Primary spines to 100 mm, triangular in cross section, shiny bright red above, white below. Aboral spines curving up slightly, ends with white shiny covering. Secondary spines present. Naked aboral interambulacral areas with blue-purple markings, bordered laterally by red lines. Test to 50 mm diameter (Fig. 24) . . . . . *Coelopleurus floridanus*

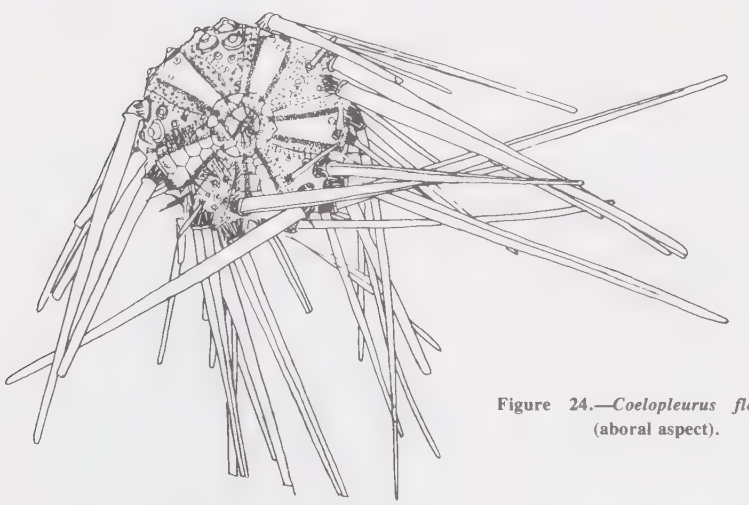

Figure 24.—*Coelopleurus floridanus* (aboral aspect).

16 (*14*) Test rarely exceeding 13 mm diameter. Depressions around primary tubercles, causing them to appear to be on raised mounds. Test surface densely covered with short spines. Periproct covered by single large suranal plate. Peristome naked except for 5 pairs of buccal plates. Color reddish or greenish with white patches ..... *Genocidaris maculata*

16 (*14*) Tubercles not surrounded by depressions. Periproct covered by numerous small plates 17

17 (*16*) Aboral primary ambulacral tubercles irregular, occurring on every plate in some columns, on every 2nd, 3rd, or 4th plate in other columns (Fig. 25). Tridentate pedicellariae with wide valves. Aboral side reddish. Test diameter to 100 mm, height 55% of diameter ..... *Echinus wallisi*

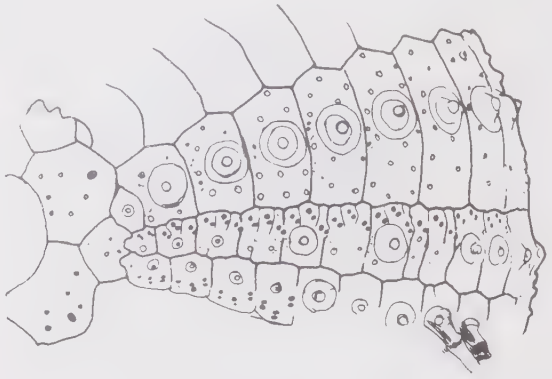

Figure 25.—*Echinus wallisi* (partial aboral aspect).

17 (*16*) Aboral primary tubercle on every ambulacral plate 18

18 (*17*) Test low (50-60% diameter), hemispherical or conical. Primary ambulacral tubercles of very unequal size in a vertical column, or if size decreases regularly towards apical system then other column of same ambulacrum not of correspondingly equal size. Tridentate pedicellariae with long (3-5 mm), slender valves. No ocular plates in contact with periproct. Color white. Test diameter to 51 mm (Fig. 26) ..... *Echinus affinis*

Figure 26.—*Echinus affinis* (partial aboral aspect).

18 (*17*) Primary ambulacral tubercles forming regularly sized series 19

19 (*18*) Test globular, height 100% of diameter. Tubercles very small. Color of test dark green, pore zones and triangular patch below each primary tubercle white, giving distinct zigzag appearance. Test to 100 mm diameter (Fig. 27) . . *Echinus gracilis*

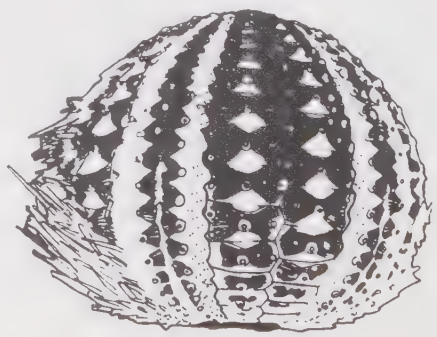

Figure 27.—*Echinus gracilis* (lateral aspect).

19 (*18*) Test only lightly tinted or white 20

20 (*19*) Test almost globular, height 75% of diameter. Sutures and tube-feet pores sunken. Regions above and below primary tubercles slightly raised, giving appearance of tubercles occurring on vertical ridges. Primary and secondary spines short and robust. Secondaries few. Test white, spines reddish. Test to 100 mm diameter (Fig. 28) ..... *Echinus tylodes*

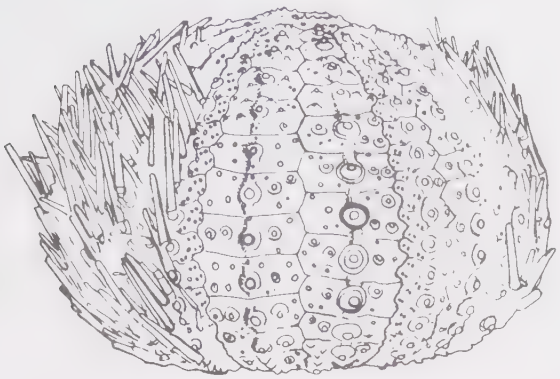

Figure 28.—*Echinus tylodes* (lateral aspect).

20 (*19*) Test low, conical or flattened above. Pores not sunken. Periproct often slightly raised. Primary spines characteristically long and slender. Primary ambulacral tubercles and spines equally sized in each column at the margin, reducing abruptly in size on upper surface. One or two ocular plates in contact with periproct. Color pink, fading to white after preservation. Test to 86 mm diameter (Fig. 29) ..... *Echinus alexandri*

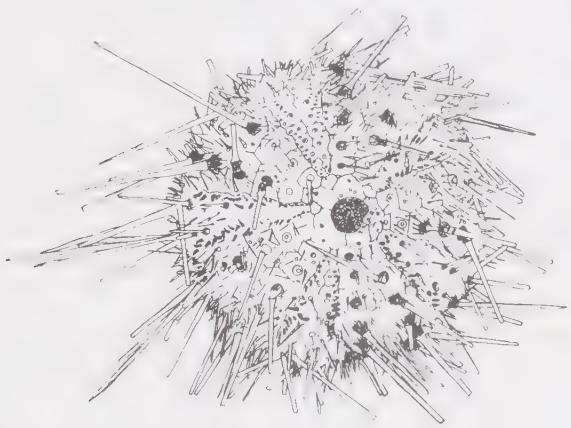

Figure 29.—*Echinus alexandri* (aboral aspect).

21 (*2*) Five lunules. Periproct on oral surface between mouth and posterior lunule. Genital pores 4 (occasionally more on aberrant genital plates). Food grooves on lower side bifurcate close to peristome. Color brown to green. Test to about 120 mm length (Fig. 30) ..... *Mellita quinquiesperforata*

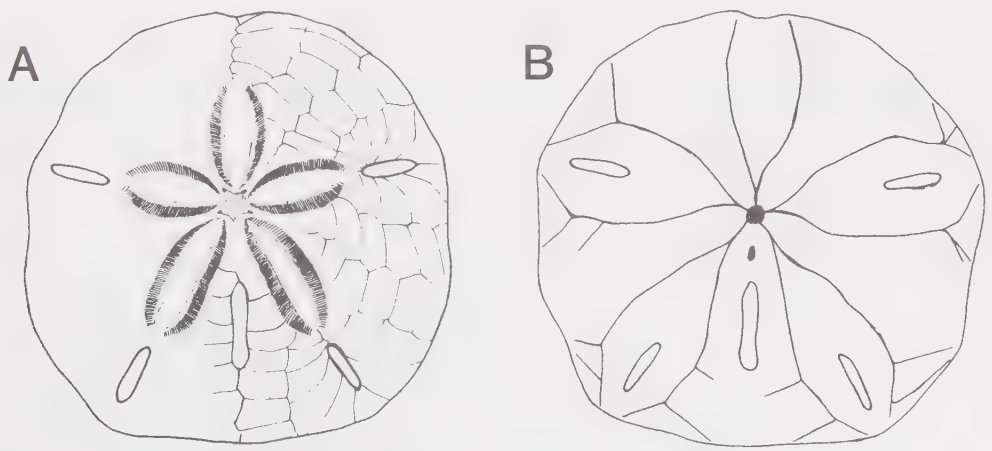

Figure 30.—*Mellita quinquiesperforata*. A, aboral aspect; B, oral aspect.

21 (*2*) No lunules. Periproct on posterior margin. Genital pores 4. Food grooves 5, straight, trifurcating towards margin. Lower side usually flat. Spines very short aborally, longest around peristome. Color red to brown, tube-feet and accessory tube-feet red (Turns almost black above and greenish below in Formalin). Test to 100 mm length (Fig. 31) ..... *Echinarachnius parma*

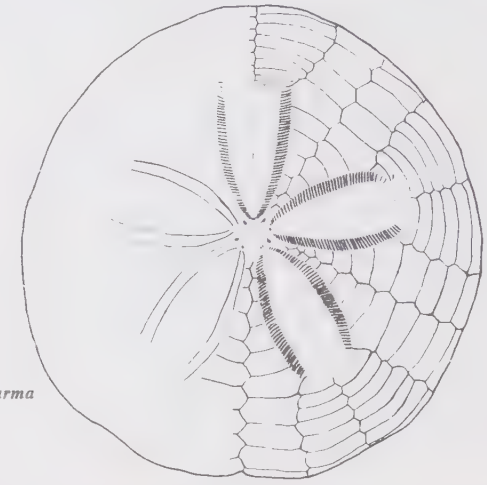

Figure 31.—*Echinarachnius parma* (aboral aspect).

22 (*3*) Aboral ambulacra simple. No petals. Labrum followed by single sternal plate (meridosternous, Fig. 4). Apical system longitudinally elongate or disjunct 23

22 (*3*) One or more ambulacra on upper surface modified into petals. Labrum followed by paired sternal plates (amphisternous, Fig. 4). Apical system compact, central 25

23 (*22*) Test bottle-shaped (Fig. 32). Subanal snout prominent, with subanal fasciole. Color purple. Length to 110 mm, usually under 50 mm ..... *Pourtalesia miranda*

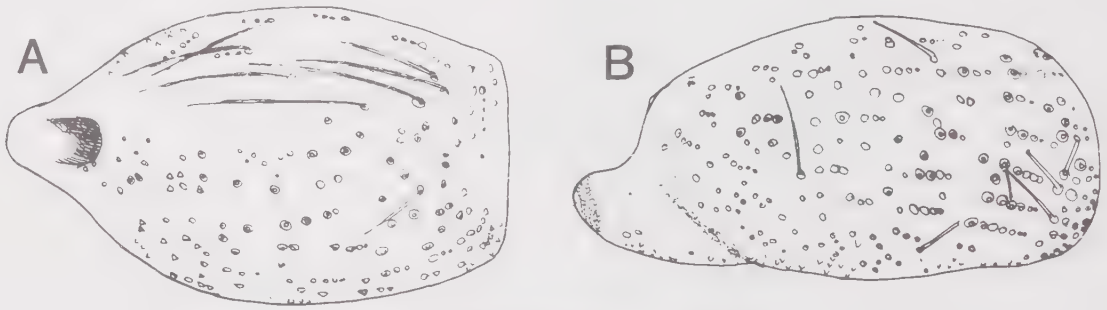

Figure 32.—*Pourtalesia miranda*. A, aboral aspect; B, lateral aspect.

23 (*22*) Test ovoid 24

24 (*23*) Lower surface flattened. Periproct submarginal, visible from below. No fascioles. Color pale brown. Length to 30 mm (Fig. 33) ..... *Urechinus naresianus*

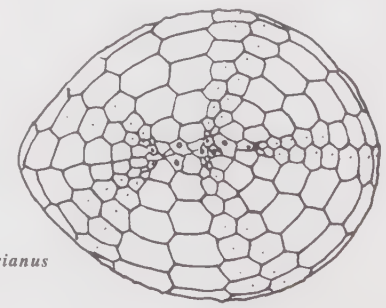

Figure 33.—*Urechinus naresianus* (aboral aspect).

24 (23) Lower posterior surface bulging, forming subanal snout, with subanal fasciole. Periproct visible from above only. Color light gray (in alcohol). Length to 20 mm (Fig. 34) ..... *Plexechinus hirsutus*

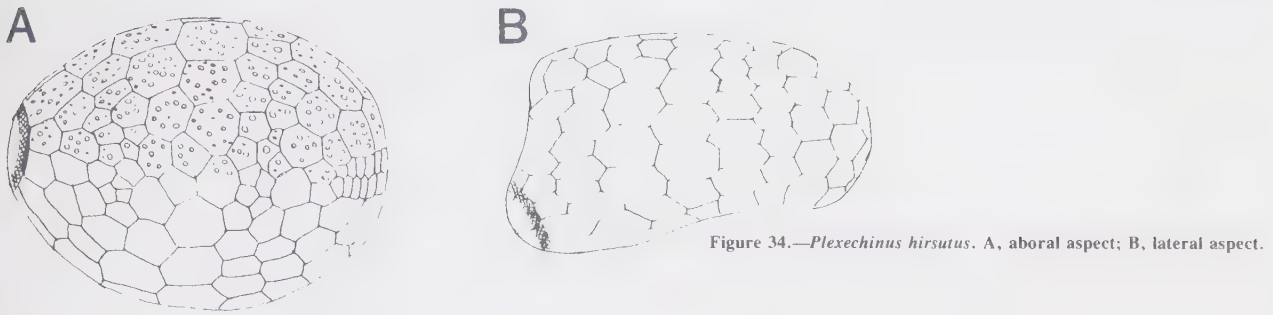

Figure 34.—*Plexechinus hirsutus*. **A, aboral aspect; B, lateral aspect.**

25 (22) Internal fasciole present, also subanal fasciole, with anal branches. No peripetalous fasciole. Test faintly heart-shaped with shallow anterior notch. Periproct high on posterior surface. Paired petals widest proximally, tapering distad. Color pale brown. Test to 92 mm length (Fig. 35). ..... *Echinocardium cordatum*

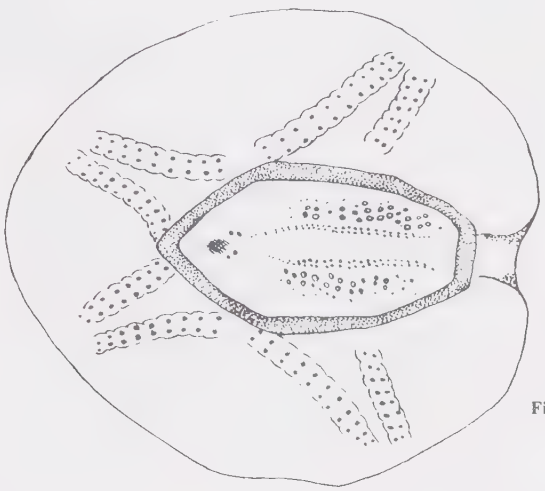

Figure 35.—*Echinocardium cordatum* **(aboral aspect).**

25 (22) No internal fasciole. Peripetalous fasciole present 26

26 (25) Only a peripetalous fasciole present 27

26 (25) Peripetalous fasciole present in addition to latero-anal or subanal fasciole 29

27 (26) Test globular, fragile, highest at posterior end. Upper surface flattened, sloping forward. Paired ambulacra strongly petaloid, petals small. Fasciole well developed. Color brown with fasciole dark when intact (denuded in picture). Length to 55 mm, usually much less (Fig. 36) ..... *Hemiaster expergitus*

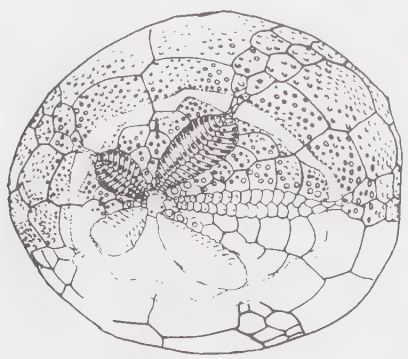

Figure 36.—*Hemiaster expergitus* **(aboral aspect).**

27 (26) Test ovoid or elongate. Frontal ambulacrum strongly petaloid, paired petals rudimentary 28

28 (27) Test elongate, almost cylindrical. Length up to 3.5 times greater than width. Frontal ambulacrum not sunken. Fasciole restricted to frontal half of test. Peristome flush on lower surface. Periproct above ambitus, visible from above. Color brown. Length to 40 mm (Fig. 37) ..... *Aeropsis rostrata*

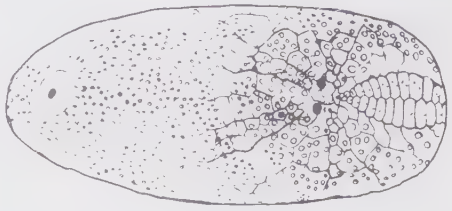

Figure 37.—*Aeropsis rostrata* (aboral aspect).

28 (27) Test low, width 50-75% of length. Frontal ambulacrum large, sunken, occupying almost half of upper surface. Frontal margin notched. Peristome vertical on front end. Periproct below margin. Color gray (preserved). Length to 30 mm (Fig. 38) ..... *Aceste bellidifera*

Figure 38.—*Aceste bellidifera* (aboral aspect).

29 (26) Subanal fasciole present, no latero-anal fasciole. Genital pores 4 in adults 30

29 (26) No subanal fasciole, latero-anal fasciole present. Genital pores 2 or 3 in adults 31

30 (29) Peripetalous fasciole single (Fig. 39A). Posterior petals confluent proximally, divergent along distal half. Test elongate oval with shallow frontal notch. Subanal fasciole kidney-shaped (Fig. 39B) sometimes with anal branches. No enlarged tubercles on upper surface. Color light brown to greenish. May exceed 85 mm in length ..... *Brissopsis mediterranea*

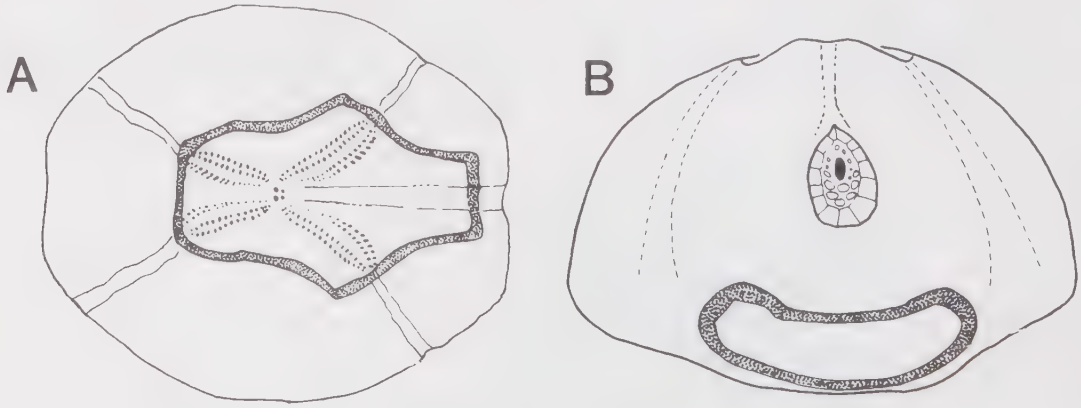

Figure 39.—*Brissopsis mediterranea*. A, aboral aspect; B, posterior aspect.

30 (29) Peripetalous fasciole doubled or tripled in places. Posterior petals divergent along entire length. Frontal ambulacrum flush with test within fasciole, sunken outside forming deep anterior notch. Enlarged tubercles on upper surface. Petals widest midway along length. Color pale purple. Reaches 130 mm length (Fig. 40) ..... *Plethotaenia spatangoides*

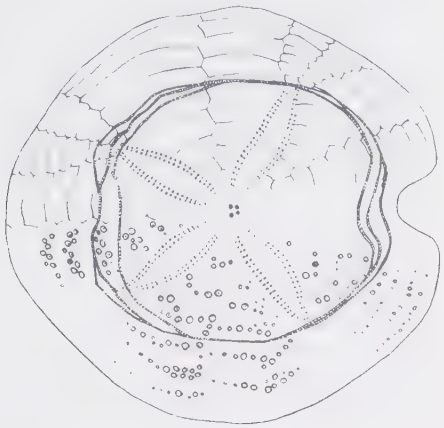

Figure 40.—*Plethotaenia spatangoides* (aboral aspect).

31 (29) Genital pores 3 in adults (Fig. 41A). Lower surface with 2 lateral bumps on posterior edge (Fig. 41B). Frontal petal large, sunken, forming deep anterior notch. Posterior paired petals 1/3 length of anterior petals. Vertical posterior margin little higher than anterior margin. Highest point of test within peripetalous fasciole. Color brown, greenish, or purplish, fasciole may be dark. Reaches 90 mm length ..... *Brisaster fragilis*

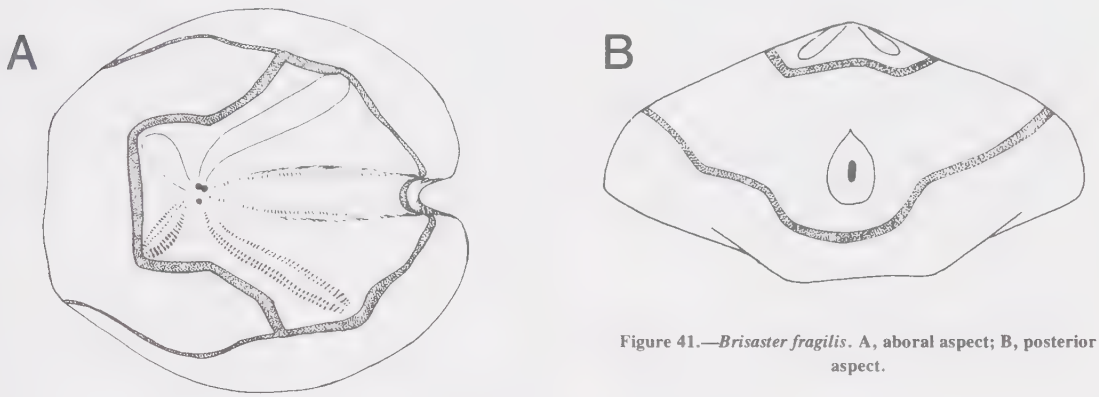

Figure 41.—*Brisaster fragilis*. A, aboral aspect; B, posterior aspect.

31 (29) Genital pores 2 in adults. Lower surface with single central bump at posterior edge. Similar to *B. fragilis* in aboral aspect. Test high, highest point at posterior end. Upper surface sloping to anterior margin, posterior edge vertical. Test white to brown, fascioles purple or black. Reaches 75 mm length (Fig. 42) ..... *Schizaster orbignyanus*

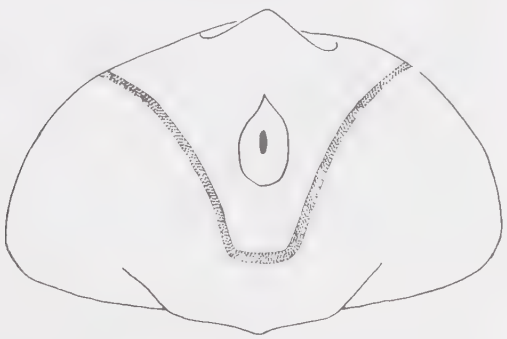

Figure 42.—*Schizaster orbignyanus* (posterior aspect).

ANNOTATED SYSTEMATIC LIST

Since the completion of Mortensen's *Monograph of the Echinoida* (1928-51), the nomenclature of the Echinoidea has been quite stable. The monograph includes complete synonymies and bibliographies for all but a few recently described species. Classification follows that of Moore (1966).

Class ECHINOIDEA
Order Cidaroida
FAMILY CIDARIDAE

These are the pencil urchins (often incorrectly called slate pencil urchins which belong in the genus *Heterocentrotus*, Echinometridae, from the Pacific). Cidaroids are primitive echinoids and are believed by many to have given rise to all post-Paleozoic echinoids. The group occurs in all seas and is perhaps most successful at present in the Antarctic.

Cidaris abyssicola (A. Agassiz 1869). It occurs off the east coast of the United States from Georges Bank (36-390 m) south to the Florida Straits. It also occurs off Yucatan and the Lesser Antilles. Bathymetric distribution is 36-800 m.

It probably occurs on firm substrata ingesting forams and other small invertebrates from the sediment surface. Small genital pores suggest it may have a pelagic larva. Worm tubes, pelecypods, and barnacles may be attached to the spines.

Stereocidaris ingolfiana Mortensen 1903. Although rare, this species has been taken widely over the North Atlantic in the Denmark Strait, off Georgia, in the West Indies, and from the North Sea to the Cape Verdes. It is yet to be taken on the New England slope. Bathymetric distribution is 300-1,745 m.

Large genital pores suggest direct development, but life history is otherwise unknown.

Order Echinothurioida
FAMILY ECHINOTHURIIDAE

The echinothurioid urchins are deep-water urchins with inflated but highly flexible tests that collapse to a disc when taken from the water. The plates are overlapping and have membranous connections rather than the rigid sutures of most echinoids. They live on soft bottoms upon which they support themselves by long, delicate, oral primary spines that are either hoofed or club-shaped. They are capable of surprisingly rapid movement. The tubercles are perforate and noncrenulate. The ambulacral plates are compounded in the diadematoid fashion but sometimes with such a high degree of modification that it is termed the echinothurioid type. As in cidaroids the ambulacral plates continue across the peristome. The secondary spines are tipped with poison glands and live specimens should never be handled with naked hands. Some authorities believe that this group is a survivor from the Paleozoic era, others that it is only a peculiar offshoot of the diadematoids. The fragile, flexible nature of the test and the deep-water epifaunal habitat result in poor representation in the fossil record.

Araeosoma fenestratum (Wyville-Thomson 1872). This species apparently occurs all over the North Atlantic from the Denmark Straits to Yucatan and Barbados and off Ireland and Portugal. It has not yet been taken north of Cape Hatteras off the eastern United States. Bathymetric distribution is 160-1,180 m.

Gut contents include bottom sediments and a variety of plant fragments.

Hygrosoma petersi (A. Agassiz 1880). This species has been taken from off Sable Island and south to off Barbados, in the Gulf of Mexico, off Ireland, the Azores, Senegal, the Bay of Biscay, and South Africa. Bathymetric distribution is 200-3,700 m (1,000-2,100 m off the northeastern United States).

The purple color is unchanged by preservation. The gut has been found to contain mud and fragments of *Sargassum* and *Thalassia* (Pawson 1982). The eggs are large and yolky, probably indicating direct development. Parasitic copepods commonly form galls on the inner surface of the test. This epibenthic species is very active and capable of relatively fast movements (Pawson 1982).

Phormosoma placenta Wyville-Thomson 1872. This species occurs all over the North Atlantic from the Davis Strait and Iceland south to the West Indies and the Gulf of Guinea. Subspecies occur in the North Atlantic (*placenta*), Caribbean (*sigsbei*), and off southwestern Africa (*africana*). Bathymetric distribution is 50-3,700 m, but it is very rare in depths shallower than 500 m (1,300-2,700 m off the northeastern United States), and the specimen from 50 m has questionable data.

The test is more rigid than that of most echinothurioids. Observations on live animals by scientists in the deep-diving submarine *Alvin* show that this species has large sacs enclosing spines on the upper surface. These are always lost in specimens collected in dredges or trawls. The species is gregarious, occurring sporadically in large groups on the sea floor. It is frequently taken in deep trawls. The eggs are large (1 mm in diameter) and yolky, implying direct development. The gut may contain mucus-bound pellets of mud, 1-3 mm in diameter (Pawson 1982).

Order Diadematoida
FAMILY ASPIDODIADEMATIDAE

This small family contains tropical deep-water urchins with small (up to 30 mm) globular tests and very long (up to 150 mm), slender spines that curve towards the substratum. The oral spines widen at the tip. This provides a footing that enables the urchins to live on soft muddy substrates with the test held well off the bottom.

Plesiodiadema antillarum (A. Agassiz 1880). This species occurs from off New Jersey (1,800 m) and Bermuda south to central Brazil in the western Atlantic and from the Canaries to southwest Africa in the eastern Atlantic. Bathymetric distribution is 580-3,700 m.

This species ingests bottom mud and detritus. Development is unknown but the eggs are small (0.1 mm or less) and it is probably indirect.

Order Pedinoida
FAMILY PEDINIDAE

Caenopedina cubensis A. Agassiz 1869. This rare species occurs south of Cape Cod (360-400 m) to the West Indies and off the Azores and Canaries. Bathymetric distribution is 250-1,200 m.

The gut contains bottom detritus, but the life history is otherwise unknown.

Order Salenioida
FAMILY SALENIIDAE

The saleniids are remarkably like the more primitive cidaroids, but are easily distinguished by their imperforate primary tubercles, lack of ambulacral plates on the peristome, and an off-center periproct which is displaced by a large suranal plate. The group is mostly fossil with only two extant genera with species mostly restricted to the tropics. The habitat and life history are believed to be similar to the aspidodiadematids (above).

Salenocidaris varispina A. Agassiz 1869. It has been taken just south of Cape Cod (900 m) and occurs south to southern Brazil in the western Atlantic. It is known from the Bay of Biscay to southwest Africa in the eastern Atlantic. Bathymetric distribution is 250-3,000 m.

Intestines contain poorly defined mud balls (Pawson 1982).

Salenocidaris profundi (Duncan 1877). This species has not yet been taken in the study area but could have been confused with *S. varispina*. It is presently known from Bermuda, off South Carolina (1,920 m), and throughout the Greater and Lesser Antilles in the western Atlantic. In the eastern Atlantic it is known from Iceland to Tristan da Cunha. Bathymetric distribution is 220-3,700 m.

Order Arbacioida
FAMILY ARBACIIDAE

The shallow-water representatives of this family occur in tropical and temperate American seas with one species extending to the eastern Atlantic.

Coelopleurus floridanus A. Agassiz 1872. This species occurs from Surinam, through the West Indies, and up the U.S. east coast to Cape Hatteras. A specimen has reportedly been taken 150 km south of No Mans Land (southwest of Martha's Vineyard) in 190 m (Harvey 1956). Bathymetric distribution is 65-2,380 m, but it is rare below 500 m.

This is one of the most beautiful urchins in the North Atlantic. The colors of red, white, and blue fade only slightly with preservation. It lives on sandy bottoms and the gut contains sand, fragments of bryozoans, octocoral spicules, and worm tubes (Lewis 1963).

Arbacia punctulata (Lamarck 1816). This species occurs from the south side of Cape Cod to the Bahamas and northern Cuba and throughout the Gulf of Mexico. A southern population occurs from Panama to Surinam, but it is absent from Hispaniola, Jamaica, the south coast of Cuba, and the Lesser Antilles north of Barbados. Bathymetric distribution is 0-225 m, but the species generally occurs in < 50 m.

This is a common sea urchin of the warmer waters of the east coast of North America. It is easily recognized by conspicuous naked median areas in the aboral interambulacra and an anal cone composed of four triangular plates. This species has been used so extensively in embryological studies that it has been the subject of a book (Harvey 1956). Most of the information below comes from this source.

The spines vary from short and stout to slender and pointed depending on degree of exposure to wave action. In many echinoid species, specimens from areas subjected to wave turbulence have short, stout spines and specimens from calm water have longer, more slender spines. The oral spines tend to be spatulate distally, an adaptation for locomotion. When removed, spines take about 2 mo to regenerate.

The color is variable. In the Massachusetts region specimens can be reddish, purplish, brownish, and sometimes almost black. Further south, very pale specimens have been taken. The color is known to change according to lighting conditions.

This species is omnivorous, although it is primarily an algal feeder. It prefers hard substrata and is gregarious, occurring in widely separated beds. In each bed, urchins tend to be of approximately the same age. Beds die out occasionally and may become reestablished later. In the Woods Hole region, *A. punctulata* is obtained by dredging in 6-30 m, but numbers have declined through the century as a result of over-collecting. Throughout its range, *A. punctulata* is subjected to temperatures ranging approximately from 2° to 30°C.

Arbacia punctulata spawns from June through August at Woods Hole, for longer periods further south, and generally year-round with a peak in fall off western Florida (Serafy 1979). Development is by an echinopluteus larva, which takes 3-4 mo through metamorphosis in the laboratory (23°C). The growth rate in nature is unknown for New England. Serafy (1979) found that urchins which had metamorphosed off western Florida in April reached a test diameter of 25 mm by the following November.

Order Temnopleuroida
FAMILY TEMNOPLEURIDAE

This family is richly represented in the Indo-west Pacific but has only three species in the North Atlantic. Members have a high degree of surface sculpture (pits, grooves, depressions, ridges, naked areas) on the test and the tubercles are imperforate. The ambulacral plates are compounded in the echinoid fashion. There are three pore-pairs to each compound plate. Many of the Pacific species are remarkably colorful.

Genocidaris maculata A. Agassiz 1869. In the western Atlantic this species occurs from south of Cape Cod (210 m) to northern Brazil. In the eastern Atlantic it occurs from the Azores and the Mediterranean Sea to off the Congo. Bathymetric distribution is 12-420 m.

This is a very small species rarely exceeding 13 mm in diameter with genital pores developing at 3-5 mm (Serafy 1979). It appears to live on sand substrates and ingests sand and small benthic animals (forams, snails, bryozoa, etc.). The eggs are very small (0.05 mm), suggesting a pelagic larva.

Order Echinoida
FAMILY ECHINIDAE

The genus *Echinus* has 18 species of which 13 occur in the Atlantic. Ten of these are restricted to the North Atlantic, which is believed to be the area of origin of the genus.

Echinus affinus Mortensen 1903. This is essentially a deep-water species ranging from Iceland south to Georgia and the Azores. Bathymetric distribution is 130-5,300 m, but it is rare in depths $< 1{,}000$ m. It has been taken in 830-2,700 m off the northeastern United States.

Scientists in the submarine *Alvin* have noted that this species is gregarious and occurs in large sporadic patches on the ocean floor. Gut contents include bottom sediment and forams.

Echinus alexandri Danielssen and Koren 1883. This is a deep-water species ranging from northern Norway and Iceland south

to off Cape Hatteras in the western Atlantic and the Azores in the eastern Atlantic. Bathymetric distribution is 365-3,120 m (830-2,700 m off the northeastern United States).

Life history is probably similar to *E. affinis* and gut contents include mud and foraminifera.

Echinus gracilis A. Agassiz 1869. This species ranges from south of Cape Cod (130-250 m) to northern Cuba, off Puerto Rico, Yucatan, and Venezuela. Bathymetric distribution is 70-450 m.

The characteristic zigzag color pattern of this species is altered only slightly by preservation and makes it immediately recognizable. It apparently prefers firm bottoms. The gut has been found to contain coarse bottom material, shell fragments, bryozoa, and sponges. Eggs are small.

Echinus tylodes H. L. Clark 1912. This species occurs off the U.S. east coast from off Cape Cod (270 m) to the Florida Straits. Bathymetric distribution is 270-810 m.

This species is easily recognized by its pink, stout spines and rather bare test. The gut contains small shells and hydroids. Eggs are small.

Echinus wallisi A. Agassiz 1880. This rare species has been taken off Georges Bank (960 m), southeast of Cape Cod (560 m), off Georgia and northern Florida. Bathymetric distribution is 460-2,600 m.

FAMILY STRONGYLOCENTROTIDAE

This family is circumarctic to circumboreal in distribution with *S. droebachiensis* (and possibly *S. pallidus*) being the only species in the North Atlantic.

Strongylocentrotus droebachiensis (O. Fr. Müller 1776). This species has a circumpolar distribution. It has been taken as far north as northern Greenland, Spitsbergen, and the Siberian Sea. It occurs intertidally north of Cape Cod but only subtidally south of Cape Cod to the mouth of the Chesapeake Bay. In the eastern Atlantic it occurs south into the North Sea (lat. 52°N). In the Pacific it occurs south to Kamchatka (lat. 54°N) and Puget Sound (lat. 48°N). It has also been taken in Hudson Bay. Bathymetric distribution is 0-1,150 m, although it is most common in < 50 m and is rare below 300 m.

As with *Arbacia punctulata*, those specimens subject to wave action tend to have shorter, stouter spines. The color of the test and spines is green, but on some specimens the spines (and more rarely the test) may be whitish. Red-brown pigment granules occur in the epidermis of the test and, if concentrated, may make the test appear red-brown, especially on the apical system and down the vertical sutures. These spots turn dark purple in Formalin. The concentration of these pigment granules is related to the consumption of red algae.

This species is mostly a shallow-water coastal species. It is found in large numbers on rocky seashores, but also occurs on sand and mixed bottom types where it tends to be more evenly spaced and more dispersed. It is omnivorous, but mostly herbivorous, preferring the brown kelp *Laminaria* sp. over other macroalgae from the northeastern United States. It is known to damage kelp beds when its concentrations are large (Mann 1977, 1982). Large numbers will aggregate to and pile up on any loose pieces of kelp on the bottom. These vigorous scavenging habits have earned it the title of "marine rodent." Adults will eat smaller specimens in aquaria.

In the New England area spawning occurs from January through April. The gonads are largest in November to April and are edible, but not especially palatable. Efforts to develop a roe fishery have met with failure. A starved urchin can live many months by metabolizing its gonads. Development is via an echinopluteus larva. Swan (1961) found that in southern Maine, *S. droebachiensis* grows to about 10 mm in 6 mo, 25 mm in 1.5 yr, 40 mm in 2.5 yr, 50 mm in 3.5 yr, and 55 mm in 4.5 yr.

Strongylocentrotus droebachiensis may be found in estuaries where the salinity does not drop below 29‰. Throughout its range, temperatures between −1.8° and 21°C are encountered. Under adverse conditions they may autotomize their spines; these take about 1 mo to regenerate on juveniles and 2-3 mo on adults. The larger urchins migrate from the tidal zone to deeper water for the winter and return in the spring. These migrations take place in a matter of 2-3 d and in Maine, they occur in mid-December and mid-May.

There is evidence based on studies involving sperm agglutination that another species, *S. pallidus*, may also occur off the northeastern United States. Jensen (1974) indicated that *S. pallidus* has more pore-pairs per arc (6-7 rather than 5-6 for *S. droebachiensis*) and globiferous pedicellariae with poison glands swollen and head spherical (compared with globiferous pedicellariae with muscular neck and head ovoid for *S. droebachiensis*). These characters are quite variable and at present there is no clear morphological distinction between the two species (Swan 1962).

Order Clypeasteroida

FAMILY ECHINARACHINIIDAE

This family of sand dollars has a circumarctic to circumboreal distribution and appears to have a single surviving species.

Echinarachnius parma (Lamarck 1816). In the North Atlantic *E. parma* occurs from Labrador to off Cape Hatteras. In the Pacific it occurs from Alaska to Vancouver Island and along the Aleutians to Kamchatka and northern Japan. Bathymetric distribution is 0-1,625 m, but specimens are uncommon below 100 m.

Echinarachnius parma can be found in large numbers from just below low water to about 100 m. It is common on substrates of coarse to fine skewed medium sands (0.8-2.2 Φ) with low silt-clay values (<5%) (Serafy, unpubl. data). Nourishment is derived from organics within ingested sand and detritus which may settle on the test and be carried to the mouth by ciliary currents. It occurs in beds of varying densities, sometimes as high as 400/m^2. Time-lapse photography off Massachusetts has shown that shallow-water populations bury themselves during the day and in winter may remain buried at night too. Throughout its range *E. parma* could be expected to encounter temperatures of −1.8° to 28°C. Spawning time can span June through November, with a peak in late summer to fall. The echinopluteus larva can be raised through metamorphosis without difficulty if fed on phytoflagellates (e.g., *Dunaliella*). Specimens under 10 mm TL concentrate the heavy mineral magnetite (Fe_3O_4) in their intestinal diverticula. This is believed to enable small specimens to remain on the bottom during high current activity. Small specimens are eaten by cod and haddock.

FAMILY MELLITIDAE

Mellita quinquiesperforata (Leske 1778). This species occurs from south of Cape Cod along the U.S. east coast, throughout the Gulf of Mexico and Caribbean Sea to Sao Paulo, Brazil. Bathymetric distribution is 0-180 m, but it is most common in < 30 m.

It lives most commonly on sand and silty-sand substrata of estuaries and inshore environments.

In Florida the larval life-span is 7 to 9 d. Specimens off western Florida reach a size of 50-75 mm test length after 1 yr and 80-100 mm after 2 yr. Spawning occurs from February to April off western Florida (Serafy 1979).

Order Holasteroida
FAMILY URECHINIDAE

Irregular echinoids with the labrum followed by a single sternal plate forming the meridosternous plastron (Fig. 4C). The first plate in each of the paired interambulacra also followed by a single plate. There are no petals, the ambulacra are essentially similar to the interambulacra. The apical system is longitudinally disjunct, with anterior and posterior portions. This is a deep-water family with representatives rarely taken in < 500-1,000 m.

Urechinus naresianus A. Agassiz 1879. This species is apparently distributed throughout the Atlantic from the Davis Strait to the subantarctic region. Bathymetric distribution is 770-5,200 m (2,300-3,100 m off the northeastern United States).

Life history is unknown. The lack of fascioles or petals and the coarse spination suggest that this species is a shallow burrower.

Plexechinus hirsutus Mortensen 1905. This species has been taken sporadically from around Iceland to the West Indies. Bathymetric distribution is 750-3,060 m (3,060 m off the northeastern United States).

FAMILY POURTALESIIDAE

These are meridosternous irregular echinoids with extremely modified test shapes and they are known as bottle urchins. The test is basically oval in shape with the anterior end truncated with a deep groove extending from the anterior ambitus to the vertical mouth on the ventral side. There is a long subanal snout and subanal fasciole at the posterior end. These deep-water urchins are very fragile and are rarely taken intact.

Pourtalesia miranda A. Agassiz 1869. This species has been taken in the Atlantic from the Davis Strait, around Iceland, and northeast of the British Isles, south through the Caribbean and into the South Atlantic. Bathymetric distribution is 450-5,850 m (1,100-2,600 m off the northeastern United States).

Pourtalesia is instantly recognized by its peculiar shape and purple color. It buries itself in soft mud and feeds on bottom sediments. Specimens of up to 50 mm in length have been taken, but some Caribbean fragments, recently recovered, indicate that they may reach a size of 110 mm. This means that most of the generic classification has been made using juveniles or small adults. There was already some question as to whether one or two species of *Pourtalesia* occur in the North Atlantic, and the absence of adult material leaves the matter unresolved at present. The northern form was described as *P. wandeli* Mortensen 1907, while the tropical form is *P. miranda*.

Order Spatangoida
FAMILY HEMIASTERIDAE

Spatangoids with the labrum followed by two sternal plates (amphisternous) forming the plastron (Fig. 4B). Paired petals are small but well developed and are surrounded by a prominent peripetalous fasciole. No other fascioles are present.

Hemiaster expergitus Loven 1874. This deep-water species has been taken from the Davis Strait south through the Caribbean to Brazil in the western Atlantic and from Iceland to southwest Africa in the eastern Atlantic. A subspecies occurs throughout the northern Pacific and has been taken off New Zealand. Bathymetric distribution is 380-4,833 m (1,102-4,833 m off the northeastern United States).

The well-developed fasciole, petals, and frontal ambulacrum suggest a deep burrowing existence.

FAMILY AEROPSIDAE

Amphisternous spatangoids with a peripetalous fasciole, well-developed frontal petal with large tube-feet, but only rudimentary paired petals. This is a small deep-water family with only two genera. The large frontal ambulacrum, tube-feet, and fasciole suggest a burrowing existence. Life history is otherwise unknown.

Aeropsis rostrata (Wyville-Thomson 1876). This species occurs in the Davis Strait, off the eastern United States, south to Cape Hatteras and Bermuda, and off Uruguay in the western Atlantic. It has been collected in the Bay of Biscay, off Portugal, and off Sierra Leone in the eastern Atlantic. Bathymetric distribution is 1,100-4,897 m (1,100-2,900 m off the northeastern United States).

Aceste bellidifera Wyville-Thomson 1877. This species has been taken in the western Atlantic from south of Cape Cod through the Gulf of Mexico, the Caribbean, to off southern South America. In the eastern Atlantic it is known from the Canaries and off Senegal. Bathymetric distribution is 550-5,220 m (1,100-3,000 m off the northeastern United States).

FAMILY SCHIZASTERIDAE

Amphisternous spatangoids with a peripetalous fasciole and a latero-anal fasciole.

Schizaster orbignyanus A. Agassiz 1880. This species occurs from south of Cape Cod (110-230 m) through the Caribbean and Gulf of Mexico to Surinam. Bathymetric distribution is 26-500 m.

It is known from bottoms of crushed shell, algal sand, and mud. Life history is otherwise unknown.

Brisaster fragilis (Duben and Koren 1844). This species ranges from the Barents Sea, off the coast of Norway, off Iceland, in the Davis Strait, and south along the east coast of North America to Georgia. Bathymetric distribution is 14-1,700 m (100-850 m off the northeastern United States).

It occurs on muddy bottoms, but life history is otherwise unknown.

FAMILY BRISSIDAE

Amphisternous spatangoids with a peripetalous fasciole and a subanal fasciole.

Brissopsis mediterranea Mortensen 1913. This species ranges from Newfoundland to the Florida Straits, off Colombia and Venezuela, in the Mediterranean Sea, and off the west coast of Africa to the Gulf of Guinea. Bathymetric distribution is 37-3,200 m

(160-2,886 m off the northeastern United States).

The life history is unknown, but is probably similar to that of *B. alta* and *B. atlantica* which have been studied in detail by Chesher (1968).

FAMILY SPATANGIDAE

Amphisternous spatangoids with only a subanal fasciole (except *Plethotaenia* which also has a peripetalous fasciole).

Plethotaenia spatangoides (A. Agassiz 1883). This species occurs from Cape Cod south through the Gulf of Mexico and Caribbean. Bathymetric distribution is 150-619 m.

The gut contains mud, forams, pteropods, small bivalves, and gastropods and it apparently lives only partially buried (Chesher 1968).

FAMILY LOVENIIDAE

Amphisternous spatangoids with an internal fasciole.

Echinocardium cordatum (Pennant 1777). This species is cosmopolitan. It is rare in the western Atlantic, but is known from off New Jersey to the Caribbean Sea. Bathymetric distribution is 0-230 m.

This species occurs in shallow water in Europe, and it has been studied extensively (Mortensen 1951; Nichols 1962; Buchanan 1966). The life history and development of this species are probably typical of most spatangoids. It lives in a burrow about 15 to 20 cm deep. A respiratory tube extends to the surface of the sea floor and is maintained by the large tube-feet of the frontal ambulacrum. A similar but blind canal extends posterior from the subanal fasciole and is maintained by the large tube-feet originating within the fasciole. The surfaces of the burrow and tunnels have a lining of mucus. The ciliated spines of the fasciole create water currents which cause water to pass down the respiratory tube onto the apical system, frontal ambulacrum, and paired petals. The water currents flow past the respiratory tube-feet of the petals over the surface of the test to the subanal fasciole which directs the water to the rear (sanitary) canal. The water flow brings suspended detritus and oxygen to the urchin.

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Coordinating Editor: Melbourne R. Carriker, College of Marine Studies, University of Delaware, Lewes, DE 19958.

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In addition to establishing the format for the "Marine Flora and Fauna of the Northeastern United States," the Board invites systematists to collaborate in the preparation of manuals, reviews manuscripts, and advises the Scientific Editor of the National Marine Fisheries Service.

We regret to report that two of the original Editorial Advisers are no longer with us: Wesley N. Tiffney passed away last year, and Roland L. Wigley has retired from professional work. We would like to express our deep thanks to both for their enthusiasm and support during the formative stages of the "Marine Flora and Fauna of the Northeastern United States" and for their many subsequent editorial contributions.

On the brighter side, we are pleased to report that two new systematists (Cavaliere and Pawson) have joined the Board of Editorial Advisers, and we look forward with much pleasure to their participation in the work of the Board. Their names and affiliations are listed above.

Many individuals have assisted the authors of the present manual in a variety of ways. Particularly to be mentioned are John H. Dearborn, University of Maine, who is overseeing the echinoderm sections of the "Marine Flora and Fauna of the Northeastern United States," and Ruth D. Turner, Museum of Comparative Zoology, Harvard University, who guided the authors in the early stages of the manual. David L. Pawson, National Museum of Natural History, critically read the manuscript. The fine echinoid collections at the Museum of Comparative Zoology, Harvard University, and the National Museum of Natural History in Washington, DC, were used extensively in the preparation of the manual. All illustrations were drawn by F. Julian Fell.

COORDINATING EDITOR'S COMMENTS

Publication of the "Marine Flora and Fauna of the Northeastern United States" is most timely in view of the growing universal emphasis on work in the marine environment and the urgent need for precise and complete identification of organisms related to this work. It is essential, if at all possible, that organisms be identified accurately to species. Accurate scientific names of plants and animals unlock the great quantities of biological information stored in libraries, obviate duplication of research already done, and often make possible prediction of attributes of organisms that have been inadequately studied.

D. Keith Serafy began his echinoid work in 1967 as a student research assistant at the Florida Department of Natural Resources Marine Research Laboratory in St. Petersburg, FL. He continued his research on echinoids at the University of Maine where he completed his M.S. and Ph.D. degrees. He maintained his interest in echinoids while conducting several environmental baseline studies on benthic communities while at the New York Ocean Science Laboratory and the Virginia Institute of Marine Science. Since 1978 he has been teaching and continuing his echinoid research at Southampton College where he is an Associate Professor of Biology and Marine Science.

F. Julian Fell started echinoid studies while an undergraduate student in the late 1960's. He completed his M.S. and Ph.D. degrees at the University of Maine, writing theses on echinoid systematics. He is presently following the precedent of Alexander Agassiz and is employed in the mining industry. As opportunity permits he is still conducting echinoderm studies on his own.

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